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EDITOR'S NOTE

At the meeting of the Committee on Publications of the Ninth Pacific Science Congress, it was agreed that the increasing number of communications and papers presented at each Congress has become a very difficult problem for the Publication Committee and the editorial staff to cope with and that too much time is required to complete the publication of the Proceedings; therefore, it was recommended that the following principles governing publication be followed:

a. That invited contributions to the scheduled symposium be published in full;

b. That reports of the Standing Committees be published in full;

c. That other papers submitted to the Congress during its sessions be published in abstract only, the abstract not to exceed 500 words;

d. That papers which, though listed on the program or included in the pre-Congress abstracts published in advance but not actually submitted to the Congress at its sessions, should be disregarded;

e. That authors be asked to indicate by a definite and early date[1] whether they prefer to publish their papers in sources other than the Congress Proceedings; that if this is done, the Congress should be acknowledged;

f. That all proof reading be the responsibility of the editorial committee, and that this committee shall consider the manuscripts in their hands by a definite date as final;[2]

g. That authors be held responsible for submitting their material in good English;

h. That on matters arising during the course of publication and not specifically covered in the statement of policy the editorial committee is empowered to act.

In accordance with the resolutions of the Committee, the editorial board has edited the reports and manuscripts where necessary to bring uniformity and consistency to the format. Typographical and grammatical errors as well as errors in phraseology, spelling, or technical terms have been corrected, wherever possible, but in cases where the exact meaning of the original copy was not clear, the text has been left as submitted by the author.

In order to reduce the cost and bulk of the publication, appendices, illustrations, and exhibits whenever considered not vital to the text have been eliminated.

If an author requested to publish elsewhere, his paper has been mentioned in the footnote under the respective titles, but if an author who presented a paper at the Congress failed to submit his manuscript either in full or in abstract, his paper and the discussions thereon have been eliminated entirely.

It was also decided that, in order to complete the publication of the Proceedings as soon as possible, each division be published in a separate volume. Short volumes or the ones that do not require too much editorial work will be released first. Therefore, among the twenty volumes planned, any volume may appear first. They will not appear in consecutive order.

The editorial board wishes to thank all authors who were prompt in submitting their revised manuscripts in good form and, in particular, members of the Standing and Organizing Committees, too numerous to be named, who have helped in collecting the manuscripts pertaining to their respective divisions.

The Board wishes in particular to thank Dr. F. Raymond Fosberg for going over and correcting the Special Symposium on *Climate, Vegetation, and Rational Land Utilization in the Humid Tropics* under Unesco;

Mr. Saman Buravas of the Royal Mines Department for helping by redrawing charts and maps in order that they might reproduce clearly when printed;

Mr. J. Alan Tubb of the FAO Regional Office, for his assistance in going over and clarifying some of the papers in the Fisheries and Oceanography volumes and in translating some of the French papers;

Dr. Pradisth Cheosakul of the Department of Science for editing the Chemistry in the Development of Natural Resources volume;

Last but not least, the Board wishes to thank the *Thai Watana Panich Press* for their cooperative efforts, far beyond the requirement of the contract, in devoting all their resources to printing these volumes.

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[1] January 1, 1958, in the case of the Ninth Congress.
[2] March 1, 1958, in the case of the Ninth Congress.

ABBREVIATIONS

APFC	—	Asia-Pacific Forestry Commission
CAA	—	Civil Air Administration
CSIRO	—	Commonwealth Scientific and Industrial Research Organization (Australia)
ECAFE	—	Economic Commission for Asia and the Far East
EQUAPAC	—	Equatorial Pacific (oceanographic survey)
FAO	—	Food and Agriculture Organization
IACOMS	—	International Advisory Committee on Marine Sciences
ICA	—	International Cooperation Administration
ICAO	—	International Civil Aviation Organization
ICSU	—	International Council of Scientific Unions
IGY	—	International Geophysical Year
IPFC	—	Indo-Pacific Fishery Commission
IRC	—	International Rice Commission (FAO)
JCRR	—	Joint Commission on Rural Reconstruction (Taiwan, China)
NORPAC	—	North Pacific (oceanographic survey)
PHILCUSA	—	Philippine Council for United States Aid
PIOSA	—	Pan-Indian Ocean Scientific Association
SEATO	—	South-East Asia Treaty Organization
SPC	—	South Pacific Commission
UN	—	United Nations
UNESCO	—	United Nations Educational, Scientific and Cultural Organization
UNICEF	—	United Nations International Children's Emergency Fund
USDA	—	United States Department of Agriculture
USIS	—	United States Information Service
USOM	—	United States of America Operations Mission
WHO	—	World Health Organization
WMO	—	World Meteorology Organization

PARTICIPANTS

ALFRED, ERIC RONALD, Zoologist, Raffles Museum, Singapore.

AUDY, JACK RALPH, Division of Virus Research and Medical Zoology, Institute for Medical Research, Kuala Lumpur, Federation of Malaya.

BAL, DATTATRAYA VAMAN, Director, The Institute of Science, Mayo Road, Bombay 1, India.

BLINKS, LAWRENCE R., Professor of Biology, Stanford University, Hopkins Marine Station, Pacific Grove, California, U.S.A.

BOLIN, ROLF L., Professor of Zoology, Stanford University, Hopkins Marine Station, Pacific Grove, California, U.S.A.

BRITTAN, MARTIN R., Associate Professor of Life Sciences, Sacramento State College, Sacramento, California, U.S.A.

BROMHALL, JOHN DEREK, Chief Scientific Officer, Fisheries Research Unit, University of Hong Kong, Hong Kong.

BRONGERSMA, LEO DANIEL, Lecturer, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

CANTELO, WILLIAM W., Staff Entomologist, U.S. Navy (Agana, Guam), FPO Navy No. 926, San Francisco, California, U.S.A.

CHRISTIAN, JOHN JERMYN, Physiologist, Naval Medical Research Institute, Bethesda 14, Maryland, U.S.A.

CLARKE, GEORGE L., Associate Professor of Zoology, Harvard University and Woods Hole Oceanographic Institution, Cambridge, Massachusetts, U.S.A.

COOLIDGE, HAROLD JEFFERSON, Executive Director, Pacific Science Board, National Academy of Sciences, 2101 Constitution Avenue, Washington 25, D.C., U.S.A.

COWAN, IAN MCTAGGART, Head, Department of Zoology, University of British Columbia, Vancouver 8, B.C., Canada.

DEIGNAN, HERBERT GIRTON, Associate Curator of Birds, Smithsonian Institution, Washington 25, D.C., U.S.A.

FEHLMANN, HERMAN ADAIR, Assistant Curator, George Vanderbilt Foundation, Natural History Museum, Stanford University, Stanford, California, U.S.A.

GIBSON-HILL, CARL ALEXANDER, Director, Raffles Museum, Singapore 6.

GROSS, BERTRAM, Chief Bureau of Rodent Control, Division of Sanitation, Territorial Department of Health, Honolulu, Hawaii.

GURJANOVA, EUPRAXIE, Head, Laboratory of the Zoological Institute, Academy of Sciences of the USSR, Leningrad, USSR.

HARDY, ALISTER CLAVERING, Professor of Zoology, Department of Zoology and Comparative Anatomy, University Museum, Oxford, England.

HARRISON, JOHN LEONARD, Zoologist, Institute for Medical Research, Kuala Lumpur, Federation of Malaya.*

HARRY-ROFEN, ROBERT REES, Research Director, George Vanderbilt Foundation, Natural History Museum, Stanford University, Stanford, California, U.S.A.

HIATT, ROBERT W., Dean of the Graduate School and Director of Research, University of Hawaii, Honolulu 14, Hawaii.

* Queensland Institute of Medical Research, Herston Road, Herston N. 9, Brisbane, Queensland, Australia.

HORMCHONG, TWEE, Instructor, College of Education, Ministry of Education, Bang Saen, Thailand.

HÖRSTADIUS, SVEN, Professor of Zoology, Zoological Institute, University of Uppsala, Uppsala, Sweden.

KAWAMURA, SYUNZO, Lecturer, Institute of Polytechnics, Osaka City University, 12 Minami-ogimachi, Kitaku, Osaka, Japan.

KHAN, M.R., Assistant Fisheries Officer, FAO Regional Office for Asia and the Far East, Bangkok, Thailand.

LEKAGUL, BOONSONG, Physician, Sahakarnbhaet Clinic, Bangrak, Bangkok, Thailand.

LIANG, HSU MU, Professor and Head, Biomorphic Department, National Defense Medical Center, Taipei, Taiwan, Republic of China.

LINDSEY, CASIMIR CHARLES, Assistant Professor, Institute of Fisheries, University of British Columbia, Vancouver 8, B.C., Canada.

LYNSDALE, JEAN A., Professor of Zoology and Dean of Science, Zoology Department, University of Rangoon, Rangoon, Burma.

MCCLURE, H. ELLIOTT, Medical Ornithologist, 406 Medical Laboratory (U.S. Forces, Japan), APO 343, San Francisco, California, U.S.A.

MACFARLANE, W.V., Professor of Physiology, University of Queensland, Brisbane, Australia.*

MEAD, ALBERT RAYMOND, Professor and Head, Department of Zoology, University of Arizona, Tucson, Arizona, U.S.A.

MEINKOTH, NORMAN A., Fulbright Foundation Lecturer, Department of Biology, Chulalongkorn University, Bangkok, Thailand.**

MEYER, KARL F., Director, Hooper Foundation, University of California Medical Center, San Francisco 22, California, U.S.A.

MILLER, ROBERT C., Director, California Academy of Sciences, San Francisco 18, California, U.S.A.

MILTON, OLIVER M.B., Conservation Specialist, Peabody Museum, Yale University, New Haven, Connecticut, U.S.A.

MUNROE, EUGENE GORDON, Principal Entomologist, Insect Systematics and Biological Control Unit, Entomology Division, Science Service, Department of Agriculture, Ottowa, Canada.

MURPHY, ROBERT CUSHMAN, Research Associate (Curator Emeritus), American Museum of Natural History, New York 24, New York, U.S.A.

PEMBERTON, CYRIL EUGENE, Experiment Station, Hawaiian Sugar Planters' Association, Honolulu, Hawaii.

ROZEBOOM, LLOYD EUGENE, Associate Professor, The Johns Hopkins University, 615 North Wolfe Street, Baltimore 5, Maryland, U.S.A.

SACHET, MARIE-HELENE, Bibliographer, Pacific Science Board, National Research Council, 2101 Constitution Avenue, Washington 25, D.C., U.S.A.

SEARLE, ANTONY GILBERT, Lecturer in Zoology, Department of Zoology, University of Malaya, Cluny Road, Singapore 10.

STEINHAUS, EDWARD A., Professor, Laboratory of Insect Pathology, University of California, Berkeley 4, California, U.S.A.

STRECKER, ROBERT LOUIS, Zoologist (Pacific Science Board), Ponape, East Caroline Islands, U.S. Trust Territory of the Pacific.

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* Australian National University, Canberra, A.C.T., Australia.

** Department of Biology, Swarthmore College, Swarthmore, Pennsylvania, U.S.A.

SUNDERLAND, SYDNEY, Dean, Medical School and Professor of Anatomy, Anatomy Department, Medical School, University of Melbourne, Carlton N. 3, Victoria, Australia.

SZENT-IVANY, JOSEPH JULIUS HUBERT, Entomologist, Department of Agriculture, Stock and Fisheries, Port Moresby, Papua.

TAYLOR, EDWARD HARRISON, Fulbright Foundation Lecturer, Department of Biology, Chulalongkorn University, Bangkok, Thailand.*

THAINEUA, MALI, Provincial Health Officer, Department of Health, Ministry of Public Health, Ubon, Thailand.

TRAPIDO, HAROLD, Deputy Director, Virus Research Centre, 20 A Wellesley Road, Poona 1, India.

UMESAO, TADAO, Assistant Professor, Osaka City University, 12 Minami-ogimachi, Kitaku, Osaka, Japan.

VAJROPALA, KLOOM, Professor of Zoology, Department of Biology, Chulalongkorn University, Bangkok, Thailand.

VANIJ-VADHANA, SUPACHAI, Professor and Head, Department of Biology, Chulalongkorn University, Bangkok, Thailand.

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* Snow Hall, University of Kansas, Lawrence, Kansas, U.S.A.

ZOOLOGY

Standing Committee Chairman: H. BOSCHMA
Organizing Committee Chairman: SUPACHAI VANIJ-VADHANA

Standing Committee Report

Editor's Note—Dr. H. Boschma, who was to have presented a formal report of the Standing Committee on Pacific Zoology at this time, was ill, and could neither attend the Congress nor prepare the report. In its place Dr. L.D. Brongersma presented a report of his own preparation.

Dr. Brongersma commented on the difficulties of biological research, especially systematic, encountered by workers in smaller countries where there are inadequate library facilities and where obtaining specific references involves considerable effort. He commented upon the geographical position of Thailand with reference to the overlap of northern and southern faunas, and stressed the desirability of intensive, comprehensive and continuing systematic work by persons in academic, government, and private positions.

A PRELIMINARY REPORT ON A COLLECTION OF LITTORAL INVERTEBRATES FROM THE VICINITY OF THE CHULALONGKORN UNIVERSITY MARINE BIOLOGICAL STATION

NORMAN A. MEINKOTH

Fulbright Foundation Lecturer, Department of Biology, Chulalongkorn University, Bangkok, Thailand.†

Chulalongkorn University completed construction of the first of a projected group of buildings for its Marine Biological Station in January, 1957. This station is located at Ang Sila (also known as Ang Hin) on the east shore of the Gulf of Thailand in Cholburi Province, about 100 kilometers southeast of Bangkok. The initial building includes living facilities for a small complement of personnel, a laboratory room, a running fresh-water system, and electricity. A caretaker lives on the premises. The littoral habitats in the immediate vicinity include rocky shores, sand beaches, mixed sand, mud and rocky bottoms, and mud flats. The water is quite turbid due to the effluence of the Bang Pakong River, the Chao Phya River and lesser streams that flow into the northeastern part of the Gulf of Thailand. Salinity fluctuations in the vicinity of the station have not as yet been determined, but it is presumed that the dilution of sea water by the rivers is considerable.

It seemed advisable to begin operations at the new station by undertaking a survey of the available marine invertebrate fauna. In the absence of more sophisticated collecting apparatus or a boat, collections were made by fine-mesh dipnet, by walking along the shores at low tide and taking specimens by hand, and by digging sand and mud with a spade and sifting it through a bamboo sieve of approximately 0.3 mm. square mesh. This last item is a common commodity in any Thai market. Specimens were placed in vials, jars or buckets of sea water and returned to the laboratory. Many were relaxed in a mixture of sea water ethanol (ethyl alcohol), sea water containing 8% $MgCl_2$, or a combination of these, prior to killing and preserving in 10% formalin or 70% ethanol. Some were relaxed and then killed in Bouin's fixing solution for future sectioning. The specimens were taken to the laboratory of the Department of Biology at Chulalongkorn University for identification and cataloging.

At this point the author wishes to express his appreciation of the help and cooperation of Prof. Supachai Vanij-Vadhana, Head of the Department of Biology and Secretary-General of Chulalongkorn University, whose efforts are largely responsible for the existence of the Marine Station, and to Mr. Twesukdi Piyakarnchana and Mr. Sunthorn Suanraksa, Instructors in Biology at Chulalongkorn, colleagues whose help as collectors and interpreters was indispensible.

At present some of the specimens have been determined to genus or family, others only to order or class due both to the exigencies of time and the unavailability of the necessary taxonomic references. No attempt at all is made here to designate species, a job for taxonomic specialists and future effort. Below is a list of animals collected on trips made between August 3 and September 1, 1957. The second column from the right indicates relative abundance. For our purposes, *rare* is employed to indicate 1 to 9 specimens taken, *common* will indicate 10 to 100 taken or available for collection, and *abundant* will indicate numbers from over 100 to many thousands collected or available for collection. No attempt is made here to indicate habitats in which the animals were found.

Porifera		
Class: Demospongia		
Subclass: Monaxonida	3 species	abundant
Cnidaria		
Class: Hydrozoa	4 sp. (medusae)	common
Class: Scyphozoa		
Order: Rhyzostomeae	1 sp.	abundant
Class: Anthozoa		
Order: Actiniaria	3 sp.	common
Order: Madreporaria	1 sp. (solitary coral)	common
Ctenophora		
Class: Tentaculata		
Order: Cydippida	*Pleurobrachia sp.*	common
Class: Nuda		
Order: Beroida	*Beroë sp.*	common
Platyhelminthes		
Class: Turbellaria		
Order: Polycladida		
Family: Prosthiostomidae	1 sp.	rare

† Department of Biology, Swarthmore College, Swarthmore, Pennsylvania, U.S.A.

Nemertea		
Class: Anopla		
Order: Heteronemertea		
Family: Lineidae	*Cerebratulus sp.*	rare
	Micrura sp.	rare
2 species of other families		
Ectoprocta		
Class: Gymnolaemata		
Order: Cheilostomata		
Family: Membraniporidae	*Membranipora sp.*	common
Brachiopoda		
Order: Ecardines		
Family: Lingulidae	*Lingula sp.*	rare
Annelida		
Class: Polydhaeta		
Family: Polynoidae	*Lepidonotus sp.*	rare
	Eunöe sp.	rare
Family: Sigalionidae	*Stheneläis sp.*	rare
Family: Nereidae	*Nereis sp.*	common
Family: Glyceridae	*Glycera sp.*	common
Family: Onuphidae	*Diopatra sp.*	common
	1 other sp.	common
Family: Spionidae	*Dispio sp.*	common
	Polydora sp.	rare
Family: Magelonidae	*Magelona sp.*	rare
Family: Capitellidae	*Notomastus sp.*	common
Family: Maldanidae	*Euclymene sp.*	common
	1 other sp.	common
Family: Pectinariidae	*Pectinaria sp.*	rare
Family: Terebellidae	*Amphitrite sp.*	rare
	2 other sp.	rare
Family: Sabellidae	1 sp.	rare
Family: Serpulidae	*Hydroides sp.*	common
	1 other sp.	common
Class: Sipunculoidea	5 sp.	common
Mollusca		
Class: Gastropoda		
Family: Nassidae	1 sp.	abundant
Family: Neptunidae	1 sp.	rare
Family: Thaisidae	2 sp.	common
Family: Muricidae	*Murex sp.*	rare
Family: Littorinidae	1 sp.	abundant
2 other families		
Class: Pelecypoda		
Family: Tellinidae	1 sp.	common
Family: Solenidae	*Ensis sp.*	common
Family: Ostreidae	*Ostrea sp.*	abundant
Family: Mactridae	1 sp.	abundant
Family: Veneridae	1 sp.	rare
Family: Mytilidae	*Mytilus sp.*	abundant
Family: Arcidae	*Arca sp.*	rare
Family: Teredonidae	*Teredo sp.*	common
Class: Scaphopoda		
Family: Dentaliidae	*Dentalium sp.*	rare
Class: Cephalopoda		
Family: Sepiidae	*Sepia sp.*	common
Arthropoda		
Class: Crustacea		
Subclass: Cirripedia		
Family: Balanidae	*Balanus sp.*	abundant
Subclass: Malacostraca		
Order: Mysidacea	several sp.	common
Order: Isopoda	1 sp.	common
Order: Amphipoda	several sp.	common
Order: Decapoda		
Family: Crangonidae	*Crangon sp.*	common
Family: Palaemonidae	*Palaemonetes sp.*	common
Family: Porcellanidae	*Polyonyx sp.*	common
	other sp.	common
Family: Albuneidae	*Albunea sp.*	rare
Family: Paguridae	2 sp.	common
Family: Cancridae	*Cancer sp.*	rare
Family: Portunidae	5 sp.	common
Family: Pilumnidae	2 sp.	common
Family: Grapsidae	1 sp.	common
Family: Pinnotheridae	1 sp.	common
Order: Stomatopoda		
Family: Squillidae	1 sp.	common
Chaetognatha		
Family: Sagittidae	*Sagitta sp.*	rare
Echinodermata		
Class: Asteroidea		
Family: Astropectenidae	*Astropecten sp.*	rare
Class: Echinoidea		
Order: Clypeastroidea	1 sp.	common
Class: Ophiuroidea		
Order: Ophiurae	*Orchasterias sp.*	common
	1 other sp.	common
Class: Holothuroidea		
Order: Dendrochirota	1 sp.	rare
Chordata		
Subphylum: Hemichordata	*Balanoglossus sp.*	common
Subphylum: Urochordata	2 sp. (colonial)	common

DISCUSSION

Dr. Taylor asked whether turbidity and fluctuating salinity may influence the composition of marine communities in the vicinity of the Marine Biological Station. Dr. Meinkoth stated that turbidity certainly excludes or impedes forms dependent upon light for orientation and navigation, and probably excludes certain filter feeders not tolerant of mud. Conversely it favors other forms well adapted to muddy environments. He remarked on the well known restrictions inflicted by varying salinities on stenohaline organisms.

Dr. Mead commented on the similarity of the forms listed with those of more northerly waters. Dr. Meinkoth agreed that in the upper part of the Gulf of Thailand many of the typical tropical invertebrates are absent, while those present are similar to a more northerly fauna. But he warned that since he is better acquainted with the northern forms his list tends to include those among the genera already identified, while the less familiar ones, in the absence of available literature, have not as yet been identified.

Dr. Gurjanova commented that the list did not agree with his previous concepts as to what tropical seas might be expected to include.

Dr. Brongersma, referring to his earlier statement about the paucity of source literature in

libraries of smaller countries, asked members to contribute and get their colleagues to contribute to the Chulalongkorn University Biology Library. He began by presenting Professor Supachai with several reprints of papers published by the Leiden Museum referring to the fauna of Thailand.

Dr. Mead asked who would ultimately identify the various parts of the collection. Dr. Meinkoth stated that he is continuing to solicit the aid of systematists in various museums and countries to undertake the determination of the various groups, and urged members present to make such suggestions as they may have regarding possible specialists who could and would cooperate.

Dr. McT. Cowan, seconded by Dr. Mead, then moved that a resolution be prepared to be presented at the next meeting urging governmental authorities in Thailand to recognize the need for extensive systematic work on the fauna of this country, and to provide the continuing financial support for its implementation. The motion was passed.

SOME FACTORS INFLUENCING DISTRIBUTION AND SPECIATION IN THE LIZARD GENUS *EUMECES*

EDWARD HARRISON TAYLOR

Fulbright Foundation Recturer, Department of Biology, Chulalongorn University, Bangkok, Thailand.

(Abstract)

The cosmopolitan lizard genus *Eumeces* with some 60 to 70 recognized species and subspecies, represents one of the most plastic and progressive groups in the Family Scincidae. It would appear however that there are two groups within the genus, one, which I believe to be the older, has representative species in northwestern India, western Asia, north Africa, and three species *(managuae, schwartzei,* and *altamirani)* in southern Mexico and Central America; the other younger one occupies China, Japan (and surrounding islands), North America south to Mexico and northern Central America.

The only other genus in the Scincidae having a large number of species (perhaps 83), that are of somewhat comparable size, cosmopolitan in distribution, and successful in maintaining large populations, is the genus *Mabuya.*

Where these two genera come together they tend to become competitors for the same kind of food, the same ecological habitats, and one or the other seems to yield territory and they tend to become mutually exclusive.

The area of eastern Asia (chiefly China and Japan) has a number of species of *Eumeces* while only a single species of *Mabuya* occupies territory, this in the southern part of the region; and no species of that genus occurs over a great part of the territory where there are several species of *Eumeces.*

In the Indo-Chinese area and eastern Thailand only a single species of *Eumeces* is known, and here the species is rare, while several species of *Mabuya* thrive. In western Thailand, the Malay Peninsula, the Sunda Islands, and the Philippine Islands, and westward on the continent through Burma and peninsular India, not a single species of *Eumeces* exists; while numerous species of *Mabuya* occupy these areas and all appear to be highly successful. Neither genus has passed eastward beyond "Wallace's Line".

In western Asia, and northern Africa from Egypt to Morocco, several species of *Eumeces* are known, while few or no species of *Mabuya* occur. South of the Sahara to the Cape, and on the great island of Madagascar there are numerous species of *Mabuya,* but the genus *Eumeces* is unknown.

In southern Canada, the United States, Mexico and northern Central America there are numerous species of *Eumeces,* all presumably belonging to the younger group. One species even passes beyond the Isthmus of Tehuantepec into northern Central America. There also occurs in northern Central America and much of Mexico (except higher parts) a species of *Mabuya,* one that is eminently successful and seemingly has a profound effect on the species of *Eumeces.* Certain species of *Eumeces,* where the *Mabuya* also occurs, have become diminutive and no longer compete for the same food, while any larger forms of *Eumeces* occupy high mountainous areas where *Mabuya* probably cannot go. The three species of the older group are presumably able to compete with the *Mabuya* (all are larger), and they are not obviously affected by its presence.

Reduction in size, lengthening of the body, and the reduction of the size of the limbs is a common expression of yielding to competition. Often survival depends on the reduction or complete loss of limbs, together with the assumption of a subterranean abode—and at the same time, a food-habitat completely different.

In summary, it would appear that *Mabuya* and *Eumeces* tend to exclude each other from food-habitats and range depending on the degree of dominance one may attain over the other. Sometimes the exclusion is not complete, as for instance *Eumeces quadrilineatus* in Thailand and Indo-China and *Mabuya longicaudata* in southern China; the presence of a single *Mabuya* in western Asia, or a single species in Mexico.

No form of *Eumeces* is known to have succeeded in becoming completely adapted to a subterranean existence. Nowhere does evidence show that *Eumeces* has succeeded in forcing *Mabuya* to change body form in order to survive, while the reverse is seemingly true.

DISCUSSION

PROF. SUPACHAI: What is the food for which the genera *Eumeces* and *Mabuya* compete?

DR. TAYLOR: Typical insects such as small coleoptera, small lepidoptera, and their larvae, diptera and their larvae, more rarely Isoptera and Hymenoptera.

CHAIRMAN BRONGERSMA: Why do you regard *Mabuya* the more dominant genus of the family?

TAYLOR: Often the greatest competitors for food and territory are closely related species. The fact that these forms tend mutually to exclude each other from certain areas show that dominance between the two groups is nearly balanced. I would suspect that in certain areas *Eumeces* becomes dominant and tends to exclude *Mabuya* completely. In other places *Mabuya* is dominent and is able to exclude *Eumeces*. In Mexico, however, one species of *Mabuya* has seemingly forced *Eumeces* to elevations in high mountains where *Mabuya* does not or cannot live. In areas where they occupy territory together the species of *Eumeces* are dwarfed, and otherwise modified. On the other hand there is no evidence that *Mabuya* has been similarly reduced.

Dr. Taylor answered questions about the interpretation of the term *dominance*, and food of the members of the genera.

Dr. Brongersma asked Dr. Taylor regarding his experience with *Eumeces*. Dr. Taylor replied that he had spent five years collecting and studying the species, preparing and publishing a monograph[1] on the genus, based on a detailed study of most of the *Eumeces* materials in American museums and much in European museums. Dr. Brongersma remarked on the difficulties presented by this genus and commended Dr. Taylor for having undertaken the project.

[1] A Taxonomic Study of the Cosmopolitan Scincoid Lizards of the genus *Eumeces* with an Account of the distribution and relationships of its species. *University of Kansas Sci. Bull.*, vol. 23, 1936, pp. 1-643, plates 1-43, text figs. 1-84.

Symposium: *Ecology and Pacific Distribution of the Giant African Snail with Special Reference to the Measures that are being taken for its Control*

A PROGNOSIS IN THE PROBLEM OF THE GIANT AFRICAN SNAIL (*Achatina fulica* Bowdich)†

ALBERT R. MEAD

University of Arizona, Tucson, Arizona, U.S.A.

Because Man is the prime vector of the giant African snail, because usually Man inadvertently carries the snails from place to place, and because Man is continually on the go, it is easy to predict that in spite of control and quarantine measures, this snail pest—the largest major snail pest in the world—will continue to be spread into many new areas within the next relatively few years.

During the last century, *Achatina fulica* was taken from its East African home to the Mascarine Islands and India. Since the turn of the century, it has traveled from Ceylon to most of Southeast Asia, fanning out in the Pacific to establish itself in a wide area from Hong Kong, Okinawa, and the Bonin Islands, to New Britain, Ponape, and the Hawaiian Islands. Actually, its frontiers have extended to Australia, Japan and continental United States; but fortunately because of interceptions and quarantine measures it has not become established in these areas. The question of prime concern is whether or not this giant snail has the capacity to establish itself in these and other uninfested areas. Little attempt has been made to answer this important question. Reasons for it rest in the fact that we know altogether too little about this animal—far less than for almost any other major agricultural pest. Most importantly, we do not know to what extent this species is able to give rise to populations containing at least a few individuals which have the physiological capacity to adjust to the reduced temperatures of the northern and southern temperate regions. The most northern population, in Ani Jima of the Bonin Islands (lat. 27° 07′ N), was found by Dr. Yoshio Kondo and myself to be in a thriving state. Apparently the threshold of minimum tolerance to cold has not yet been reached. The inordinate sensitivity of this snail to higher altitudes seems to stem not from the factor of cold alone but quite likely from intolerance to a diurnal temperature fluctuation beyond a point where to survive, it normally would need a period of several days to become conditioned physiologically. It is significant that snails are surviving colder winter temperatures at sea level in Ani Jima than they can at an altitude of 5,000 ft. in Ceylon.

What we do know about the snail tells us that we are up against a remarkably hardy pest. It lives for at least five years. During this period of time, a single individual theoretically can give rise to over five quadrillion offspring. This snail can go for a year without food and water. Since it is a scavenger, it will accept as food almost an unlimited range of items. It will bury itself several inches below ground to escape the effects of cooler weather. It has exceedingly few natural enemies. It is essentially nocturnal and crepuscular in its habits, hence escaping the rigors of diurnal life and escaping detection of its worst enemy—Man—until all too often it is inextricably established. Acid soils and their lack of available lime are no barrier; for the snail gets its lime supply by scavenging on the fallen leaves of trees that have unlocked the bound calcium in the soil. As demonstrated so beautifully by Howes and Wells (1934) in other species, this snail *irrespective of the nature of external conditions*, is subject to periodic phases of estivation due to a physiological "hydration cycle." This permits at any time inaccessible, estivating individuals to restock an infested area after the effects of natural or man-made adverse conditions have dissipated. Knowledge of this phenomenon is of tremendous importance because it gives an explanation for the failures of even some of the most rigorous control

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measures and helps us understand why this pest, after becoming firmly established, has never been eradicated. And lastly, this snail species is genetically variable to the extent that each of the different types of environment, in which the snail has been able to establish itself, appears to have had a selecting effect upon the complement of character determiners that happened to be present in the original snail stock infesting the area. Undoubtedly, the high reproductive potential of the snail has considerably accelerated this process. The results are such that a taxonomist, not knowing the whole story, would be tempted to designate the different types as distinct subspecies. We do not know the limits of genetic potentiality in producing still different and still more hardy individuals.

There is little doubt in my mind that it is only a matter of time until *Achatina fulica* becomes essentially ubiquitous in the greater share of the Indo-Pacific region. Any uninfested island or coastal continental area in the Pacific region which has even a modest cover of vegetation and which falls between 30° North and 30° South latitude must be considered a potential site of establishment for the giant snail. This includes northern and much of eastern coastal Australia, as Harrison (1951) agrees. Northern New Zealand and southern Japan lie in the peripheral regions where the possibility of successful establishment of this pest depends upon the genetic potentialities of producing more hardy types. Although my opinions have been challenged, I still feel certain that at least the southern part of California would be susceptible to invasion by this snail. The agro-climatic analogues established by Nuttonson (1952) support my earlier statements that the portion of the United States bordering the Gulf of Mexico is vulnerable to attack. It follows that much of the Neotropical region is similarly vulnerable. That the snail is not yet known to be established in the vast tropical areas of the Western Hemisphere is almost miraculous. The frontiers of invasion will be extended into desert and more temperate zones through Man's activities in building nurseries, greenhouses and desert gardens.

Chemical control measures are for the most part expensive, impractical or only transitory in effect. A truly effective, economical molluscicide has yet to be found. The currently popular metaldehyde and calcium arsenate leave much to be desired. Actually, there is evidence that improper use of mulluscicides will bring about an increase rather than a decrease of the snail population! Hand collecting and destroying is the most economical method of control and the one most often resorted to since the only expense involved is labor. Attempts to control the snails through legislative action are of limited value. Nonetheless, this "limited value" is absolutely indispensable in the overall program in providing a "holding action" until more effective control measures can be devised. Legislative action has been particularly effective in the Hawaiian Islands and California. There is little immediate hope for any appreciable controlling action through the use of the giant snail for human consumption; but experiments recently completed at the University of Arizona attest to the fact that the dried snail meal holds great promise as a poultry and livestock food supplement. Any extensive use for this purpose is certain to produce a controlling effect.

The use of multiple predators in an attempt to control the giant snail is at present being tried on an impressive scale in the Hawaiian Islands. Although it is too early to make any predictions, the results are bound to be significant. No true parasite of *A. fulica* is known. However, a disease syndrome was found to be present in snails in Ceylon, Singapore, Hong Kong and Hawaii. The epizootiological picture suggests that it is a chronic disease, producing visceral and dermal lesions and reducing the life expectancy of the snails. The disease either goes into a fatal, acute stage later in the life of the host or has a decisive effect when there is a compounding of stress factors. A.U.S. Public Health grant is making it possible to conduct experiments in an attempt to determine the etiology, the pathogenicity, and the effect of stress factors on the progress of the disease.

It is felt that this disease plays the major role in the frequently observed and reported "decline" in the older populations of *A. fulica*. The decline is so pronounced in some sections of Ceylon that the giant snail appears to be virtually extinct. When a disease agent of sufficient virulence builds up in a snail population that has passed through its normal sigmoid growth stage, the decline in the population is such that the snail ceases to be a major pest. Any subsequent recrudescence apparently is only partial.

It is not impractical to entertain the idea of using a disease agent in the biological control of *A. fulica*. In contrast to a metazoan predator, it is possible for a microbiological agent to have the reproductive capacity, virulence and transmissibility to produce a catastrophic and even

eradicative effect upon the host population. But unless the agent has a truly remarkable genetic stability, by the same token, it may produce strains with undesirable traits. Those who have worked with myxomatosis in Australia will vouch for this point. It goes almost without saying that before any use of a disease agent can be made safely, a tremendous amount of research must be done in close coordination with the microbiologist, the malacologist, the biological control man, and the naturalist. If Man is ever to eradicate the giant African snail on anything but the smallest scale, he will do it through the use of disease agents in conjunction with supplementary measures.

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DISCUSSION

N.A. MEINKOTH: Have you ever eaten this snail?

A.R. MEAD: Yes, but while edible it is not palatable. It has a strong humus flavor.

H.M. LIANG: Japanese forces ate them during World War II. It is claimed that eating a large amount causes vomiting.

A.R. MEAD: They are standard items of diet in Ghana and interior Taiwan. No distress is suffered. Excess snail meal in chick feed gives chicks diarrhea. But when they recover, they gain faster than control chicks.

H.M. LIANG: They are used to feed ducks on Taiwan.

J.L. HARRISON: They are thought in Malaya to give a bad taste to duck eggs and flesh.

A.R. MEAD: There is convincing evidence that snails in the diet induce ducks to lay more eggs, and it is clearly shown they do not change the flavor of the eggs.

J.L. HARRISON: *Achatina* in Malaya seems confined to cultivated areas and does not occur in the bush or forest.

A.R. MEAD: It is an enigma why snails do not enter the native bush extensively. Yet they readily enter paces disturbed by man, and survive quite a while after he abandons it, but do not seem to penetrate far peripherally.

J.L. HARRISON: In Malaya they survive in abandoned resettlement clearings for quite a while.

A.R. MEAD: May I point out the genetic flexibility of these and other snails? Dwarf populations occur in many places. Variation in the disease syndrome which I observed may be due to genetic differences in the snails or the disease agents, or both. Adaptibility is great, and environmental selection factors are also great, which results in great differences among populations.

W.W. CANTELO: Many variations are noted in Micronesia.

J.L. HARRISON: Is this genetic variation or simply lack of complex environmental selectivity?

S. HORSTADIUS: Have any genetic studies been undertaken?

A.R. MEAD: No, but they are contemplated for the near future.

S. HORSTADIUS: Would it be valuable to make such experiments on a large scale?

A.R. MEAD: Yes, it would.

S. HORSTADIUS: In using snail-meal for chick feed, is there any use to which the shells can be put?

A.R. MEAD: Yes, they are used in the chick feed to some extent. In places they are buried. But they may have a profound effect on soil pH to the disadvantage of certain crops, such as tea.

C.E. PEMBERTON: Are there any other diseases useful in control of *Achatina*?

A.R. MEAD: Practically nothing is known about this subject. A few papers are published on apparent gastropod pathogenesis, but results do not rule out senescence or malnutrition.

E.A. STEINHAUS: In France, there is an *Aerobacter* infection in cultured *Helix*.

A.C. HARDY: Are electric fences used to keep snails out of areas?

A.R. MEAD: Although this would work, it is not a practicable procedure.

A.C. HARDY: Are there any natural bird predators in Africa, especially those eating eggs or young?

A.R. MEAD: Many birds do, but avian predators are categorically ruled out because of other considerations.

R.L. STRECKER: On Ponape a decline in the snail population followed the introduction of the barrier fence. The question is, how good are census methods?

A.R. MEAD: Sound sampling methods have been developed and tested.

FURTHER COMMENT: *Achatina* has been known in Ceylon for 50 years. The disease has recently built up, and snails are disappearing locally. In Hawaii the disease incidence rose from 17% to 56% in three years. If the disease along with environmental stress reduces the population, the snails should cease to be a major pest.

R.L. STRECKER: I question the value of the carnivorous snail *Gonaxis* in control.

A.R. MEAD: Its value is not proved. Where *Gonaxis* has been introduced *Achatina* has declined, but populations of *Achatina* have also declined where *Gonaxis* was not introduced. The question remains as to how to evaluate *Gonaxis*.

C.E. PEMBERTON: How long have the giant snails been on Agiguan?

A.R. MEAD: It is believed that they were introduced in 1946 or 1947, but it may have been somewhat earlier.

W.W. CANTELO: Were they on Saipan and Tinian before the war?

A.R. MEAD: Yes. They came to Saipan about 1938. They were brought to Guam about 1946. These snails were introduced for use in primitive medicine, later got loose and became pests. The same thing happened in Hawaii; they were advertised by Japanese enterpreneurs and sold.

E. GURJANOVA: During the war a large marine snail was introduced into the Black Sea, its eggs deposited on ship hulls. It now is very abundant.

A.R. MEAD: This is comparable to *Achatina;* also to the introduction of the marine snail *Littorina littorea* in many parts of the world.

S. VANIJ-VADHANA: What is the pest status of *Achatina* in Malaya?

J. L. HARRISON: It does not seem to be a serious pest.

S. VANIJ-VADHANA: That seems to be the case in Thailand.

A.R. MEAD: It is recent in Thailand. In Malaya it was not a pest at first, later became a serious pest in some places, but now has subsided considerably.

J. L. HARRISON: It seems to have reached an equilibrium.

A.R. MEAD: This is the history of growing populations of all kinds.

W.W. CANTELO: Populations are subsiding on Guam and Marianas. We no longer find giant forms, more medium sized ones. People put bait out in open places, attract snails out where sun can kill them. I think the problem is vastly overrated.

A.R. MEAD: This thinking is common, and in some places justified. Nevertheless under certain circumstances it can be a very serious problem. There is no need to panic, but the problem should not be underrated. In Ceylon they seriously damage cacao seedlings, and many other young plants while ignoring adult plants of the same species.

R.L. STRECKER: Is the disease in Hawaii the same as elsewhere?

A.R. MEAD: Not certain; there are some differences, but these may be strain differences.

C.E. PEMBERTON: All *Achatina* in Hawaii are the progeny of 11 snails. The disease must have been brought in with them unless it is of another source.

A.R. MEAD: The origin of the disease not certain. It may have come from Africa, but it probably came from Ceylon and India. It is chronic, not acutely fatal, but fatal under stress conditions. Now we must find these stress conditions.

W.W. CANTELO: Does the disease really shorten their lives?

A.R. MEAD: This is the only logical conclusion I can reach. In Ceylon, where they have been established for 50 years, I can only find 2 and 3 year old snails, while elsewhere they may live 5 to 6 years.

At this point Dr. J.J.H. Szent-Ivany of the Department of Agriculture, Stock and Fisheries, Port Moresby, Territory of Papua and New Guinea, came in to comment on the work of a colleague, Dr. Bridgeland. In New Britain *Achatina* has become widespread and a great pest with cacao seedlings. The seedlings were circumscribed with a ring of methaldehyde in paraffin oil spread on the soil. It was very effective in attracting and killing the snails. But the process is uneconomical in the rainy season when it has to be repeated frequently.

He noted that on New Guinea the snails have not spread so fast as on New Britain, where the snails seem to be getting smaller and smaller, with none of the big ones remaining. The shells seem to be weaker, as shown by the ease with which they crush underfoot.

A.R. MEAD: Where populations are fulminating they do great damage. Persons coming into an area at a later time completely miss the crux of the real problem. When *Achatina* comes into equilibrium with various environmental factors it becomes a much smaller problem.

STUDIES ON CONTROL OF THE GIANT AFRICAN SNAIL ON GUAM†

GEORGE D. PETERSON, JR.‡

Agricultural Extension Service, University of California, El Centro, California, U.S.A.

(Abstract)

The giant African snail, *Achatina fulica* Bowdich, became established on Guam during World War II. An attempt in 1946 to eradicate the snails was unsuccessful.

The following control investigations are described:

Chemical controls: Sodium Arsenite; metaldehyde and calcium Arsenate; combined rat and snail bait; poisonous whitewash and wood ashes.

Other artificial controls: Salt water and hand-picking; barriers.

Biological control: Carnivorous snails *(Gonaxis kibweziensis)*; Indian glowworm *(Lamprophorus tenebrosus)*.

Other natural enemies: Rats and coconut crabs; musk shrew; ducks.

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‡ Assistant Agriculturist, University of California Agricultural Extension Service, El Centro, California. (Formerly staff entomologists for the Guam Department of Agriculture from April, 1951, to May, 1955.)

Symposium: ***Present Status of our Scientific Knowledge of Rodent Pest in the Pacific Area with Special Reference to the Control of Rats and of Plague***

THE RATS OF SINGAPORE ISLAND

A.G. SEARLE and S.S. DHALIWAL

Zoology Department, University of Malaya, Singapore.

The island of Singapore lies only 1° 20′ North of the equator and covers an area of about 200 square miles, being 27 miles long and 14 miles wide. It is separated from the mainland of Johore by narrow straits about half a mile across. This isolation is lessened by two main factors: the wide causeway which now connects the island with the mainland of Malaya and the vast quantity of shipping visiting the port from all over the world. In the last 150 years there has been a rapid change in the island's ecological characteristics. Instead of being sparsely populated and almost entirely covered by primary jungle, it now contains well over one million people while only a small patch of the original jungle is left. These changes have had a profound effect on the island's rats, leading to the extinction of some species, but the introduction and multiplication of others, especially those human commensals which come under the heading of pests. They may also lead to evolutionary modifications of particular species, especially when combined with some degree of isolation. A detailed study of the island's rat population and its various components should be of interest to zoologists and others concerned with public health. By comparing the results with earlier reports from Singapore and with data from the mainland, we can obtain a dynamic (if somewhat speculative) picture of present trends and thus can predict future probabilities. The present investigation has involved trapping rats in a wide variety of habitats, from city fringe to secondary jungle; we have been greatly helped by the City Health Department and by Captain Jennings of the R.A.M.C. Hygiene Unit, who have kindly supplied us with rats from urban and other areas.

Five species of *Rattus* have been recorded from Singapore, namely *surifer*, the spiny-backed rat; *annandalei*, or Annandale's rat; *norvegicus*, the brown rat; *exulans* (= *concolor*), the little Burmese rat; and *rattus* itself. *Rattus surifer* is a jungle species; its subspecies *leonis* was described by Robinson and Kloss from Singapore in 1911 but has been discovered nowhere else, suggesting that, despite its proximity to the mainland, the island has produced distinct forms. It seems doubtful whether *Rattus surifer* still survives on the island; we were unable to catch any. Sub-species *leonis* has been unable to adapt itself to the rapidly changing environment and is therefore on or over the verge of extinction.

Rattus annandalei bullatus has a much softer fur than *Rattus surifer*, and looks rather like *Rattus rattus jalorensis* (the Malayan field-rat) except that it is larger, with a skull-length of 47-48 mm. as a rule. It is quite common in some rural areas; we caught it in an old overgrown rubber estate, in belukar (scrub) and in the secondary jungle of the Nee Soon catchment area in the centre of the island. *Rattus annandalei annandalei* is known from near Kuala Lumpur in Malaya, but seems much less common there. Mainland specimens generally have a much whiter belly-color than Singapore ones which are cream or pale yellow. Thus there may be a North-South cline for ventral fur-color. Our Singapore specimens have a mammary formula of $2+2=8$ while J.L. Harrison (1948) gives $3+3=12$ or $3+2=10$ for those from the mainland. Intraspecific variation in mammary formula is usually rare; these differences suggest that more than one species may be involved. It is interesting to note that sub-species *bullatus* was originally recorded as a separate species, *Mus villosus*, by Kloss (1908).

Rattus norvegicus is a pest in many parts of the world and was no doubt introduced into Singapore soon after its foundation. It is abundant in the city harbor area and streets adjacent to this, but is hardly ever found more than half a mile or so, inland. We have not found it at all in the rural parts of the island. This is in striking contrast to the situation in Europe, where *Rattus*

rattus is confined to dock areas but *Rattus norvegicus* spreads throughout the countryside.

In the city area, two other kinds of rat are found, namely *Rattus rattus diardii* (the Malayan house-rat) and *Rattus exulans*. All three species may be caught in the same street, but in this environment *norvegicus* seems at least three times as common as the other two species conbined, some figures by Gilmour (1934) show how common rats were in Singapore city even 50 years ago. Well over 100,000 were destroyed each year, with a peak of 181,807 in 1908. Gilmour observed that there were, on the average, more fleas on *Rattus rattus* in Singapore than on *Rattus norvegicus*, although the latter is much larger. We found, however, that about 40% of *norvegicus* rats had tapeworm cysts *(Taenia echinococcus)* on the liver, but only about 10% of *rattus* rats, while none were found on *Rattus exulans.*

Rattus exulans is widely distributed on the island, not only in the city area and in kampongs outside the city, but also in belukar far away from any human habitation. We did not find it in secondary jungle.

In the past, only form *diardii* of *Rattus rattus* has been reported from Singapore, where it seems to be much more variable than on the mainland. It occupies a wide range of different habitats, such as the city area, belukar, rubber plantations, mangrove edge and even in secondary jungle. It was found far away from any houses, in sharp contrast to the situation on the mainland, where it is replaced by form *jalorensis* in such habitats. *Diardii* also shows great variation in its ventral fur-color, which may be light brown, light grey, dark smoky grey, buffy white or nearly as white as the sharply defined underparts of *jalorensis*. This variation may have been due to the absence of *jalorensis* from the island, allowing *diardii* to spread into habitats which the former would normally be better adapted for, and, perhaps relaxing selection for one particular shade of ventral fur-color. Unlike all previous workers, however, we did discover *jalorensis* on the island. All came from a restricted coastal region of mangrove (containing *Pandanus*, *Avicennia*, *Rhizophora*, etc.) on the north side of the island about half a mile west of the Singapore-Johore causeway. None were found in other favorable habitats such as belukar or secondary jungle, or in mangrove to the south of the island. Trapping on the mainland roughly opposite the *jalorensis* locality on the island produced more of the same form. These findings suggest that *jalorensis* is a recent addition to the Singapore fauna; in fact it may have spread to South Johore comparatively recently. Perhaps this is the start of a large scale invasion of the island by this form, but it may well be prevented from occupying its usual habitats by the prior presence of *diardii*. Singapore *jalorensis* show various differences from those of the Kuala Lumpur area; for instance, Singapore *jalorensis* have darker dorsal surfaces than Kuala Lumpur *jalorensis* and the dorsal stripe is more prominent in Singapore *jalorensis*.

The Table gives the statistics of body and skull sizes in Singapore rats, which may be of interest to workers in other regions. Summing up, we can see that Singapore rats exhibit many interesting biological phenomena, mainly as a result of the rapidly changing environment. There is the extinction of one form *(Rattus surifer)* due to the destruction of its habitat; the spread of species commensal with Man, such as *Rattus norvegicus* and *Rattus rattus;* the spread of a form *(diardii)* into unusual habitats owing to the absence of competition; the recent appearance of a new form *(jalorensis)* in the area, with intra-specific competition as a probable result; the genetic differentiation of populations from those in adjacent regions, and so on. Continuing studies of the rat fauna of Singapore should help us to understand these processes and to find better methods of controlling these ever menacing rodent pests.

Table. Adult Singapore rats: mean body and skull sizes in mm. with standard errors.

Species	Number	Head + body	Tail	Hind-foot	Ear	Skull-length
Rattus annandalei	10	198.0±3.3	217.9±2.1	37.8±0.6	20.9±0.3	47.7±1.2
Rattus exulans	26	111.4±1.8	128.9±2.4	23.2±0.2	16.0±0.2	30.3±0.4
Rattus norvegicus	44	222.7±3.1	191.5±2.7	42.1±0.3	20.5±0.2	47.2±0.5
Rattus rattus diardii	58	184.4±1.7	186.9±1.9	35.2±0.2	20.4±0.1	41.5±0.2
Rattus rattus jalorensis	15	176.9±2.6	151.8±4.3	32.7±0.3	19.8±0.3	40.6±0.9

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DISCUSSION

J.L. Harrison commented on the microevolution of *Rattus annandalei.* Too few specimens are available to be certain of its exact status, but he suspected a cline from Kuala Lumpur south to Singapore.

RATS IN NEW ZEALAND: A PROBLEM OF INTERSPECIFIC COMPETITION

J.S. WATSON

Animal Ecology Section, Department of Scientific and Industrial Research, New Zealand.

New Zealand has three rat species: *Rattus exulans* brought to the country by the Polynesians about 700 years ago; and *R. norvegicus*, and *R. rattus* brought by the Europeans in the first half of the nineteenth century; *norvegicus* was associated particularly with whalers who established shore stations where rats became very numerous. *Exulans* has been widely distributed over most of the country, but disappeared rapidly from the North Island at the same time as *norvegicus* became common, and it was generally assumed that the latter had driven out the former. However, in the South Island *exulans* persisted for much longer, particularly in the forested parts of the north-west and perhaps also in the south-west. At irregular intervals these rats increased tremendously in numbers and hordes of them invaded the settled districts. These rat outbreaks were most probably correlated with years of prolific seeding of the beech trees *(Nothofagus)* in the forest, and certain forest birds, particularly the parakeets *(Cyanoramphus)* were reported as being very numerous at the same time. At least four such outbreaks are known to have occurred between 1872 and the last in 1888 (Watson, 1956). It is tempting to explain the cessation of these outbreaks as a result of the introduction of mustelids at about this time in an attempt to check the spread of the introduced rabbit. In the twelve years from 1884 to 1895 over 6,000 stoats and weasels were liberated, some of which spread rapidly into the forests.

On Raoul Island in the Kermadec Group, 600 miles north of New Zealand, *norvegicus* has virtually replaced *exulans*. In a recent publication (Watson, 1956), I assumed that *norvegicus* arrived on the island during the last war, but evidence has recently come to light showing that this species came in a ship wrecked there in 1921; *exulans* was still numerous there down to 1944 but has not been found since. It is of some interest that it should have taken as long as twenty years for the one species to replace the other on an area of about eleven square miles. To-day in New Zealand, *exulans* is numerous only on outlying islands where neither of the other two rat species occurs. On the two main islands it is extremely uncommon and in recent years it has been found only in the forests of the south-west. There is also an interesting record of one being caught in the same trap line as *rattus* on Stewart Island where *norvegicus* also occurs.

Rattus is present throughout the country: in towns where it is an important pest economically, and in the indigenous forests where it feeds on fruits, seeds and insects. The three color forms of this species, usually given the subspecific names: *rattus*, with black back and grey belly; *frugivorus* with brown back and creamy-white belly; and *alexandrinus*, with brown back and grey belly; all occur in New Zealand. It is probably better outside Asia to consider them as forms of a polymorphic species rather than as separate subspecies. The grey-bellied *alexandrinus* is rare except on Stewart Island in the south, and in the forests on the west of the South Island. The pale-bellied *frugivorus* type is the commonest both in towns and forests. The black *rattus* type forms about 20 per cent of the population.

Norvegicus is widely distributed throughout the country. As is to be expected, the largest populations occur in towns, particularly around rubbish dumps and similar places; but this species is also found well away from towns, around farm buildings in the country and even along creeks on the edge of forested country far from human habitation. Accounts of this species swarming in the southern forests seventy five years ago are possibly due to confusion with *exulans*. *Norvegicus* is the only species present on the subantarctic Campbell Island.

A survey of rat infestations was carried out by the writer in industrial premises in the town of Christchurch five years ago. Both *rattus* and *norvegicus* were present; neither could be said to be dominant though *rattus* tended to be economically the more important as it was the commoner occupant of food stores and buildings, particularly above ground level. The infestations of neither species were on the whole serious and many environments potentially suitable for rats

were not occupied, and this in the absence of any very active control measures.

Christchurch is similar both climatically and structurally to many English towns where to-day *norvegicus* is the only species present. The problem arises : why, if *norvegicus* has ousted *rattus* in England, it has not done so in the New Zealand urban environment also? It is not a matter of time; both species have now been in New Zealand for well over 100 years. But in less time than this, *rattus* had almost disappeared in England following the introduction of *norvegicus* (Barrett-Hamilton, 1912), though in the United States *norvegicus* is still spreading at the expense of *rattus* (Ecke, 1954). Control measures in New Zealand may have been biasing the situation in favor of *rattus* since at the time of the survey the proprietory brands of poison bait most commonly available on the market contained either "antu" or red squill, both relatively ineffective against this species. At least one instance was discovered where an infestation of *norvegicus* was cleared out, only to be replaced by one of *rattus*. The intensity of control, however, was insufficient by itself to have accounted for the general situation.

One big differences between New Zealand and England is that in New Zealand, *rattus* is also an inhabitant of the forests which it appears not to have been in England, possibly because this ecological niche was already filled by other woodland rodents. For competition between two species to be a reality, there must be an insufficiency of a common necessity such as food or cover to meet their joint requirements. The impression gained at the time of the survey in Christchurch was that the populations of neither species were being limited by shortage of food or suitable habitat, so that in effect there was probably very little competition between them. Without competition there was no obvious reason why the two species should not both have been present in the same town. Presumably in the past there would have been periods when both species were competing, and at such times *norvegicus* would have spread at the expense of *rattus*. But the existence of the rural *rattus* population would have provided a source for the replenishment of the urban population when the intensity of interspecific competition diminished. In any case, there is a tendency for *rattus* to invade houses in autumn with the onset of colder weather.

Exulans is reported from several Pacific Islands as having been driven out or its numbers greatly diminished as a result of the introduction of one or other of these two rat species. Most of these reports should probably be treated with some caution, particularly as *exulans* (*hawaiiensis*) on the Hawaiian Islands was generally considered prior to its rediscovery in 1917 to have been replaced by the other two species (Stone, 1917). Two relatively recent first-hand accounts of biological surveys, on Raroia atoll in the Tuamotus (Morrison, 1954), and in the Marquesas (Mumford, 1942), report *exulans* being replaced by *rattus*. On the other hand, population studies that have been carried out on Guam (Baker, 1946), New Caledonia (Nicholson and Warner, 1953), and Hawaii (Spencer and Davis, 1950) have shown *exulans* living together with *rattus;* in the last two places *norvegicus* is also present.

The problem of interspecific competition among rats is extremely complex. All three species have quite distinct ecological requirement, which in South East Asia keeps one separate and enables the other two to co-exist in close proximity. However, the segregating mechanism preventing competition, breaks down under different conditions. In the Pacific there is a multiplicity of islands with various habitats, and different combinations of the three species of rats. Moreover, on some, *rattus* and *norvegicus* are only comparatively recent arrivals as a result of the last war. Here, therefore, is a unique opportunity for the collection of information to elucidate this problem.

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DISCUSSION

H.J. COOLIDGE: An interesting paper; we should hear more later on the concurrence of *Rattus rattus* and *R. exulans*. I am surprised that Watson puts the date 1921 on the introduction of *R. norvegicus* to New Zealand.

J.L. HARRISON: This date refers to the introduction to one specific island.

J.J. CHRISTIAN: Competition between *R. norvegicus* and *R. rattus*, or between any other pair of species not necessarily competitive for food, harborage or other ecological features, may be competitive on a social basis, i.e., larger and more aggressive species will drive off a less aggressive species as shown by the work of Barnett with the species cited here.

M.H. SACHET: Is there evidence for extermination of *R. exulans* from Funafuti?

J.L. HARRISON: I cite Watson's reference to Waite, 1897, Mammals, Reptiles and Fishes of Funafuti.

M.H. SACHET: I suggest a misinterpretation of this paper by Watson, because *R. exulans* was taken on that survey.

PACIFIC ISLAND RAT ECOLOGY PROJECT

ROBERT L. STRECKER

Pacific Science Board, National Research Council, Washington, D.C., U.S.A.

(Abstract)

The Pacific Science Board of the National Academy of Sciences—National Research Council has sponsored a three year program of basic research on rats as they fit into the environment of the tropical Pacific islands. The study is centered on Ponape, E. Caroline Islands, U.S. Trust Territory of the Pacific, with work being carried on in several areas of the Trust Territory.

The field program began in 1955 and will continue until 1958. This report describes the organization, procedures, and general findings of the research to date, including information on species present, geographic distribution, reproduction, sex ratios, parasites, predation, home range, food habits, swimming ability and general behavior. Detaileddata are not yet fully available since the project is still in progress.

DISCUSSION

H.E. MCCLURE: Is the short-eared owl an introduced species on Ponape?

R.L. STRECKER: Not as far as we know.

H.J. COOLIDGE: It is an indigenous species. Would metal bands on coconut trees be of use in keeping out rats on Ponape?

R.L. STRECKER: Yes, in groves planted in an orderly manner, and if bands are attached properly to the trees. Bands do not work on cacao, as they eventually kill the tree by girdling.

R.L. STRECKER: I have not seen this employed and doubt if it would work.

B. GROSS: On Tahiti metal bands are credited with increasing copra crop 30 to 40%.

A.G. SEARLE: Does *Taenia taeniaeformis* also occur in *R. exulans*?

R.L. STRECKER: Yes.

J.L. HARRISON: Lungworm and other parasite burdens probably contribute to rat mortality in live traps in times of environmental stress.

A.R. MEAD: On Saipan, Evders and I found moribund rats. Have you found them?

R.L. STRECKER: No.

H.J. COOLIDGE: Was there any interference from African snails in trapping?

R.L. STRECKER: Not especially. Sometimes snails, toads, and rain spring traps. In the Marshalls hermit crabs were a great interference.

J.L. HARRISON: Termites make it impossible to employ wooden traps in Malaya.

ECOLOGY OF THE FORMS OF *RATTUS RATTUS* IN THE MALAY PENINSULA

J.L. HARRISON

Zoologist, Institute for Medical Research, Kuala Lumpur, Federation of Malaya.

Outside South-east Asia there is a growing realisation that although the house-dwelling *Rattus rattus* may sometimes be black, and sometimes be brown, these color forms are but strains in a continuously interbreeding population of house-rats. The names *Rattus rattus rattus* for the black form and *Rattus rattus alexandrinus* for the brown form have little to recommend them, for the black rat is probably no more than an example of "Industrial Melanism" now so well described in British Moths (e.g., Ford 1945).

The distinction between the black and the brown strains has, however, obscured a difference which I consider to be more fundamental—that between the "dull bellied" and the "white bellied" forms. In the Oriental Zoogeographical region, where the species must have originated, there are many named forms of rats which are commonly regarded as being forms of a single polymorphic species *Rattus rattus.* Various attempts have been made to assemble these into series, with varying success, and to over-simplify these ideas we may quote Ellerman (1947) who says, of *Rattus rattus:* "In this species there are two main types, one of which is dull bellied and mainly parasitic, and the other of which is white bellied and wild. Both types may occur together." With that statement I have no quarrel, so long as "wild" is not taken to imply "a native forest form".

Let us consider the state of affairs in Malaya. Here among seventeen species of the genus *Rattus* we have three, *R. jalorensis*, *R. argentiventer*, and *R. diardi*, which are commonly regarded as forms or subspecies of *Rattus rattus. R. jalorensis* is a white-bellied rat of woodland; *argentiventer* is a grey-bellied rat of grassland, including rice fields; *diardi* is a dull-bellied house rat. Their habitat has been summarized by Harrison (1957).

Primitively the Malay Peninsula is forested, and two thirds of the Federation of Malaya is still covered with substantially undisturbed forest. After ten years experience in collecting rats there, I have no hesitation in saying that *R. jalorensis* does not occur in primary forest and is not one of the eleven species which can fairly be regarded as native to Malaya. Its habitat is typically the scrub which results when the forest is felled (and the native fauna driven away), and the land is neglected. It also occurs in the "imitation" forest made by man when he plants rubber, oil palm, coconut palm, or thatch palm trees.

In large areas of Malaya the primitive swamp forest has been felled, and the cleared land used for growing rice. In other parts, land cleared but not cultivated has been seized by the cosmopolitan grass *Imperata cylindrica* which is perpetuated by burning. It is these two forms of grassland, ricefields and *Imperata*-grass, that *Rattus argentiventer* inhabits and it will be noted that both habitats are man-made.

In the region of Kuala Lumpur, *Rattus diardi* is essentially a house rat. It is the principal rat in houses, forming 72% of some 10,000 animals trapped by municipal rat-trappers in Kuala Lumpur (the only other rat being *R. exulans* 2%); it is rarely found out-side of houses, and is never found far from houses (rarely more than 50 metres from a house).

This is the state of affairs in the part of Malaya near Kuala Lumpur. We have three quite distrinct members of this *Rattus rattus* complex. Each inhabits an ecologically distinct habitat, and each of these habitats is man-made. There is no sign of any member of the complex in primary forest. Furthermore, the three rats are distinct, morphologically, and appear to breed true. There is no sign of overlap or intermediates. In other words, in Malaya these three rats behave as good species.

There is nothing new in what I have been describing. A very similar state of affairs was described for Java nearly thirty years ago by Kopstein (1931) while Sodhy (1941) attemps to arrange all of the forms of *Rattus rattus* known to him into three "ecological sections" of which the three forms mentioned above are the Malayan representatives. He includes a fourth, the "Lugens-section" for a number of forms for which he has no ecological data, and which, being entirely unknown to me, I propose to omit from consideration for the time being. Generally speaking we can say that this threefold division is recognisable throughout Malaysia,

and that at least two of the divisions (those corresponding to the Malayan white-bellied *jalorensis*, and the dull-bellied *diardi*) are to be recognised in most of the Indian, and Indo-chinese regions. The Philippines appear to possess *argentiventer* (Clark, *in press*) I am not clear as to the relative status of the many forms named, but the threefold division is recognisable (Clark, personal communication).

The difficulty arises when we try to express these ideas in conventional taxonomic terms. One school of thought would wish to regard the three sections as "ecological subspecies" of *Rattus rattus*, another would wish to regard all the local forms as subspecies, and to assemble the subspecies into "ecological sections." Sody (1941), who tries the latter course, remarks that "in some regions these groups can, in other regions cannot, be distinguished as regards morphology. In the south eastern of the Lesser Sunda Islands the animals of thet hree Java sections are hardly distinguishable . . . East of Celebes the sections merge almost completely. Animals from those regions largely agree in colour and in number of mammal with the western house rats . . . These rats occur in houses but apparently they are the common field rats at the same time."

Similar difficulties are found when we go to the north and west. In Southern China (e.g., Hong Kong) there is a white-bellied field rat (*sladeni*) and a dull bellied house-rat (*flavipectus*) (Romer *in litt.*). The latter appears indistinguishable from *diardi;* there is no sign of *argentiventer.* In Burma, however, there is no dull-bellied rat at all. The *Rattus rattus* complex is represented by a white bellied rat (*khyensis*, etc.) which is typically found in such places as bamboo clumps, and is secondarily a house-rat (Harrison and Woodville, 1948). Otherwise the house-rat appears to be *Rattus exulans*, with sometimes Bandicoot rats burrowing in the floor. Hinton (1918), in describing the results of the Indian mammal survey, states that only white-bellied forms were obtained from Assam, Burma, and Tenasserim, while Audy *et al.* (1953) and Roonwal (1949) mention only the white bellied *R. bullocki* (probably a synonym of *brunneusculus*), even from houses and villages, near Impal in Manipur.

In India the picture presented by Hinton (1918) is of a wealth of local forms of the white bellied type, typically from open countryside, and an exceedingly variable population of dark-bellied forms associated with houses. Dark-bellied forms only were found from Kutch, eastward to Gwalior, southward through Bombay to Bellary, while dark and white-bellied forms occurred together in Kathiawar (Saurashtra), the old Central Provinces (Madhya Pradesh) Mysore, and parts of the Punjab at the foot of the Himalayas. From Ceylon, Travancore, up the east coast to Orissa, and Bengal only white bellied forms occurred.

Finally, in the Mediterranean region the common form is a dull bellied house-rat but a white bellied form *(frugivorus)* is to be found living "wild" in trees, where it is a pest in plantations of carob and olive trees for example.

The difficulty is, therefore, that while in Malaysia we can distinguish three entities, distinct both morphologically and ecologically, as we leave Malaysia we find that morphology and ecology no longer agree, and our classification breaks down.

These difficulties arise, I think largely because of two assumptions which are made, perhaps unconciously, by many of the writers on this subject. These assumptions are (1) that the morphological grouping (e.g. into dull and white belley) and the ecological grouping (e.g., into house and field rat) should necessarily agree; and (2) that the white-bellied rat is a native (Chasen 1933).

Let us consider what happens when we leave that part of Malaya immediately around Kuala Lumpur. First, let us go south, to Singapore. Here, as my colleagues from the University of Malaya have explained (Dhaliwal and Searle *in press*), *Rattus argentiventer* does not occur. *R. jalorensis* has been recorded but it is rare. *R. diardi*, however, is most abundant, and lives in all three of the habitats which, near Kuala Lumpur, have their own characteristic form. Thus *diardi* lives in houses, in grassland without contact with houses, and in scrub and secondary woodland. Also we have to consider another rat, *R. annandalei*, a white-bellied rat obviously closely related to *jalorensis*, which, near Kuala Lumpur, is very rare and appears to be confined to forest edge. In Singapore it is the common inhabitatant of secondary forest.

Now what happens if we go east, from Kuala Lumpur across the mountains to the central plains and the east coast? This is a region with few inhabitants, of small villages and few even moderately sized towns. I must speak with caution because my knowledge is not as extensive as I would wish, but it appears that *diardi* is hard to find. The house rat of villages is either *jalorensis* or the little *R. exulans* (which is also a rat of grassland and scrub). Even in the town of Kuantan

(23,000 inhabitants) a recent collection produced only one specimen of *diardi*, although *R. exulans*, *R. norvegicus*, and *Mus musculus* were caught. It would appear that *R. diardi* is but little established as a house rat on the East Coast, and that *R. jalorensis* functions effectively in its place. This leads us to read, in a new light, a remark by Chasen (1933) who says, of the collection of skins of *diardi* in the Raffles Museum, Singapore, "owing no doubt to the luck of collecting, the collections examined contained no specimens from Peninsular Siam, Kedah, Kelantan, Trengganu, Negri Sembilan, and Malacca". That is to say, none from the whole of the East coast of Malaya down to within about 100 miles of Singapore. It may well have been the luck of collecting, but it may equally be an indication that *R. diardi* has only recently established itself on the East side of the Peninsula.

Let us finally travel to the islands in the Straits of Malacca. There are a fairly large number, many of them covered with dense forest which at first sight appears to be typical primary forest. I have personal knowledge only of three groups, the Sembilan Islands, near the coast of Malaya, Jarak, in about the middle of the Straits, and Berhala close to Sumatra. As has been explained by Wyatt-Smith (1953), the forest on the islands of these three groups is unlike that of the mainland and resembles rather that of an oceanic island. It is suggested that at some time in the past these island have been entirely denuded of life, perhaps by a fall of volcanic ash, and that the present fauna and flora is the result of chance introduction. The rodent fauna agrees with this idea. None of the mainland forest species occur, and the only rat is, in each case, a member of the *Rattus rattus* complex. On the Sembilans, close to Malaya, and on Berhala, close to Sumatra, the rat is very close to *R. jalorensis* although the Sembilan form has been named as a separate subspecies (Robinson and Kloss, 1911). On Jarak, right in the middle of the straits, and not normally visited by fisherman, the rat is distinct and appears to me to be more nearly allied to *R. diardi* than to *R. jalorensis*, (Harrison 1950).

Here, then, are all of the anomalies which we find outside Malaysia presented within Malaya. *R. diardi*, a typical dull-bellied house rat, may be found in grassland and scrub on Singapore Island, and in forest on Jarak. *Jalorensis*, a typically "white-bellied and wild" type of rat, is never a truly wild (i.e., forest) rat in the Peninsula, and is a common house-rat on the East side, but in the island of the Malacca Straits it is a forest rat.

We can explain these anomalies in Malaya by assuming that the three members of the *Rattus rattus* group, *jalorensis*, *argentiventer* and *diardi* are three distinct species, each commensal, which have each separately been introduced into Malaya. *Jalorensis* would have been introduced first *as a house rat* with peoples moving down, coastwise from the north. It found the native *annandalei* inhabiting forest edge and replaced it almost everywhere except in the far south. *Argentiventer* was introduced with rice perhaps from Java. Finally *diardi* is a recent introduction from Southern India, introduced as a house-rat of towns to the newly settled island of Singapore, which *jalorensis* had not, at that time, reached. Thence it spread with good communications up the West coast, and completely replaced *jalorensis* as a house rat, but failed to compete successfully with the latter in scrub and plantations, so that *jalorensis*, originally a house-rat, now appears to be only a rat of scrub. The Islands near the shore were colonised early by *jalorensis* carried by fisherman, at a time when it was the only house rat, but the more remote Jarak was colonised by a dull-bellied rat carried on sea-going ships.

I can perhaps best sum up by giving an Hypothesis, and I must emphasize that it is only a hypothesis, to account for the three of *Rattus rattus* which we have been considering.

I suggest that the original form was a white-bellied, semi-arboreal rat living somewhere in India or Burma, perhaps in the Ganges plain. This rat came into contact with man in an early agricultural culture, and became adapted to the habitat provided by forest clearing, scrub, and flimsy houses of bamboo and thatch, perhaps built on stilts, as are so many houses in South East Asia. Spreading by man's unconscious agency this form rapidly colonized the cultivated areas and its fringing scrub throughout India and Burma, up into China, down into Malaysia, and westwards, through Persia into the Mediterranean. At that time there would have been an almost continuous belt of cultivation and scrub crossing the present desert areas. Westward and Northward spread would be rapid into well-settled areas, but spread to the South-east would be slow, into areas then largely covered with forests with very few scattered clearings.

This white-bellied, semi-arboreal form developed two adaptions to life in the open treeless areas, where animals have perforce to live in

burrows, instead of tree-nests, and typically have a dull coloured belly. Although dull bellies are associated with house-rats they are also to be found in those murids which live in the open grassland rather than in woodland.

Thus in the British Isles the grass-eating Voles (Microtinae) tend to be dull bellied in contrast to the so-called field mice *(Apodemus)* which in fact live in woods and hedgerows and are pale bellied. Within the genus *Apodemus* the species *A. agrarius,* which tends to live in the open is somewhat darker-bellied than *A. sylvaticus* which tends to live in woodland (Allen 1940).

Of the two dull-bellied forms in the *Rattus rattus* group one was adapted to tropical grassland and ricefields, and has spread over Malaysia as *argentiventer*. The other adaption was probably to steppe country in South western Asia, and this secondarily became adapted to life wholly in the substantial houses which, by this time, were being built from Egypt to Mohenjo Daro. This was the present dull-bellied house rat.

With the dessication of South western Asia, the white-bellied form tended to disappear leaving the present discontinuous distribution shown in the figure and the dark-bellied form became the only form to be associated with man there. It spread westward into Europe (where a wholly black form was developed) and thence by

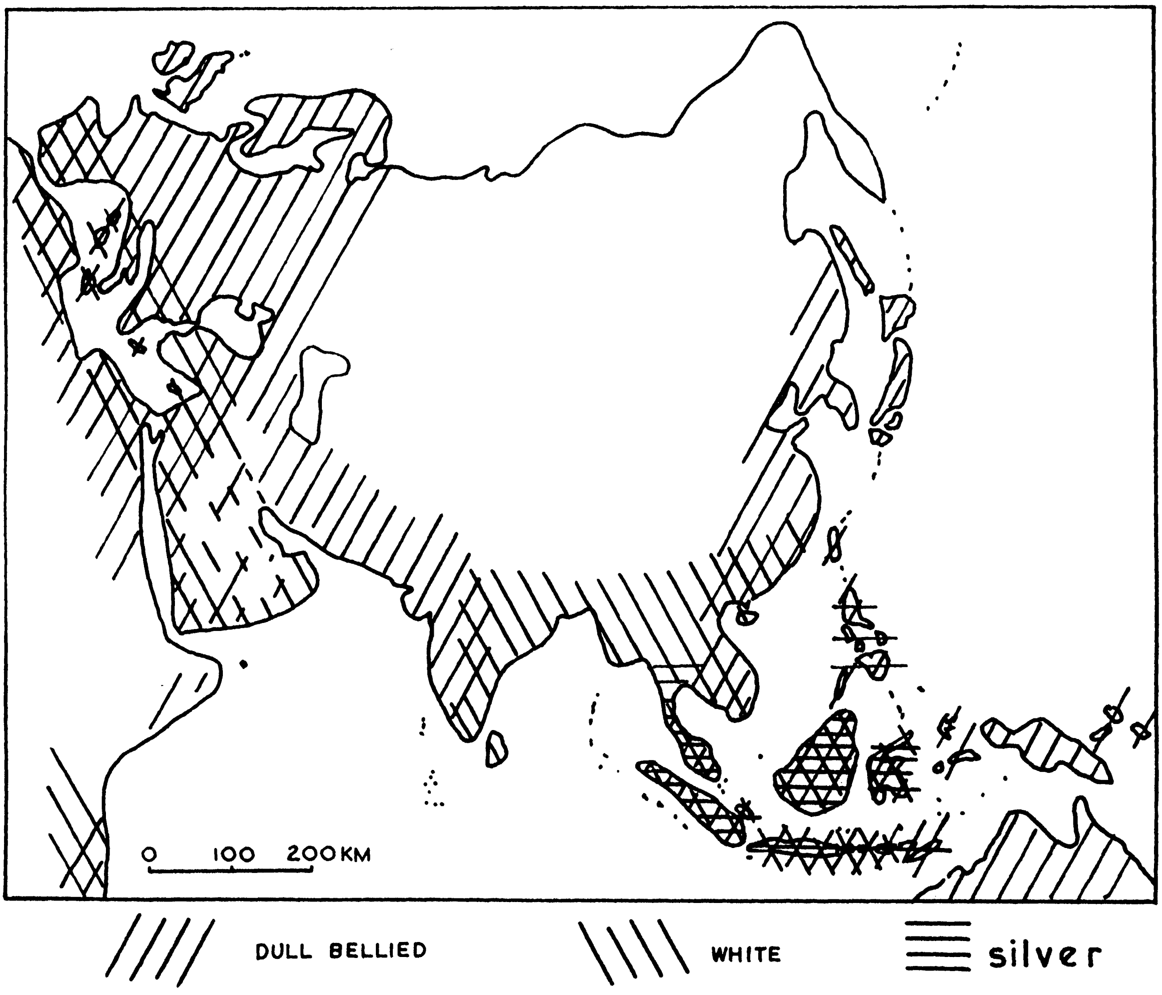

Fig. 1. — Distribution of the three "forms" of the *Rattus rattus* group in the area considered.

European shipping to America, South Africa, and more recently every seaport in the world. Eastward it spread into India where it is still spreading over the central parts. It spread down the West Coast and thence, by shipping, across to Malaysia, where as the above records show, it is still spreading. From Malaysia it spread North up to the Eastern coast to Southern China. To the Eastward it overtook and replaced the still spreading white-bellied form at the Celebes, replaced it as the house-rat, which is the form most readily spread by man, and then spread to New Guinea and the adjacent islands where it is present as a variable, apparently "local" from. Australia, on the other hand, would have been colonized by the form from Europe.

SUMMARY

1. In Malaysia rats of the *Rattus rattus* group can be divided into three kinds, a dull-bellied house-rat *(diardi)*, a silver-bellied grassland and ricefield rat *(argentiventer)* and a white-bellied woodland rat *(jalorensis)*. No member of the group is native to forest.

2. Outside Malaysia this threefold morphological and ecological classification breaks down. It is not usually possible to distinguish three forms, and the members of any one morphological type may appear in the "wrong" habitat.

3. Detailed studies in Malaya suggest a solution. Here the threefold division is found near Kuala Lumpur on the West Coast, but elsewhere one or more of the members may be missing, and the other members of the group occupy the habitat normally associated with it.

4. It is suggested that the three forms are best regarded as three species of *Rattus*, each of which is a commensal with man, which have been separately introduced into Malaysia and which have not yet wholly occupied the area.

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DISCUSSION

R.L. STRECKER: There is the puzzling situation in color variations of roof rats. A black phase and all intergrades are found on islands investigated.

J.L. HARRISON: I have seen no black phase rats in Malaya. We usually think of black phases in cold countries, but this negates such a supposition.

A.G. SEARLE: Does *R. norvegicus* spread outside port areas anywhere in the tropics?

B. GROSS: Yes, if you consider Hawaii in the tropics. It spreads to cane fields, even up into mountains.

J.R. AUDY commented on the parasite burden and diseases in rats.

R.L. STRECKER: On Ponape *Capilleria* and other worms do occur but not as heavy burdens. Some are parasite-free.

H.J. COOLIDGE: Are there any studies on the relations between rats and crabs?

J.L. HARRISON: Very little.

E.H. TAYLOR: In the Philippines the rat's diet varies from place to place. Where they eat crabs the rat-size seems larger. Samplings anywhere in Malaya should take into consideration populations of *Ptyas korras*, *P. mucosus*, and *Zaocys carinatus*, the three rat snakes.

J.L. HARRISON: Snakes are killed in Malaya around residential areas. *Rattus jalorensis* near gardens are about twice as long as those in scrub where snakes are numerous, suggesting destruction of snakes alters the mode of life of the rat.

J.R. AUDY commented on the introduction of rats into Berhala, their health condition and predation.

H.J. COOLIDGE: Are there any estimations of the cat population?

J.R. AUDY: The cat population is not great, but they are the only predators there.

H.J. COOLIDGE: In swimming tests, rats are sometimes taken by turtles and fishes.

I MCT. COWAN: commented on the occurrence of rat parasites on islands, that they are introduced along with the host, and that changes in host diet affects host resistance. Health and population density go together.

A.G. SEARLE: Differences between health and numbers of rats on Berhala and Jasah may have been because they were at different stages of the population cycle.

J.L. HARRISON: There seems to be a five year cycle for grassland rats.

THE BIOLOGICAL BASIS OF RODENT CONTROL

JOHN J. CHRISTIAN and DAVID E. DAVIS

Naval Medical Research Institute, Bethesda, and the Division of Vertebrate Ecology, The Johns Hopkins School of Hygiene and Public Health, Baltimore, Maryland, U.S.A.

INTRODUCTION

The premise of this paper is that rodent control, to be successful, must be based on the sound application of biological principles in a systematic attack on a population of a given species. Much evidence under-scores the statement that the most effective way to reduce a population and maintain it at a reduced level is to increase intraspecific competition (Davis, 1949). Recent research has made it evident that competition, or social pressures, induces physiological responses which have a suppressive effect on the growth of populations. The balance of this paper will be a more detailed account of such a chain of events along with a summary of the experimental evidence for its existence. However, it should be born in mind that predation by man or other predators (in the broadest sense) has been generally ineffective in the sustained control of populations. In fact the usual poisoning or trapping campaign, unless maintained at a continuously very high level of intensity, usually results in an increased reproductive rate following the initial reduction in population size with a resultant rapid return to (or above) the original level (Davis, 1949, 1951; Barnett, 1952). For example, where populations of rats in Baltimore City were reduced by trapping to 50 to 90% of their initial levels, there was an initial rate of recovery of 4% of the maximum per month which later slowed to 2% a month as the population approached the initial level (Emlen, Stokes, Winsor, 1948). The data of these authors clearly show a relationship between population density and the rate of recovery following decimation of the population. Poisoning campaigns usually are unsuccessful even with sustained effort, due to the development of bait shyness on the part of the rats (Barnett, 1952).

We clearly recognize that there will be considerable variation in the details of methodology with different species and different environments, and that it will be necessary to know the life history of an animal in a particular environment in order to know the best way to increase competition effectively. For example, rat control in urban areas can be achieved by general sanitation which increases competition by reducing the available supplies of food and harborage. However, as Barnett points out (1952), sanitation of this sort is not generally practicable for rural populations. Hence other methods of increasing competition must be sought. Nevertheless the general principle will remain the same: achieving population control by increasing competition even though the means may vary.

The limited information available in 1953 on the effects of competition on population growth permitted only one page to be devoted to this subject in a 22-page review of the characteristics of rat populations (Davis, 1953). Nevertheless it had been apparent for some time that competition was an important factor in the regulation of rat populations (Eaton and Stirrett, 1928; Calhoun, 1949; Davis, 1949, 1951). It had already been shown that reducing the size of a rat population resulted in increased reproduction and growth in the survivors (Davis, 1949). A mechanism involving physiological responses to population density capable of explaining how competition exerted its effects was hypothesized in 1950 (Christian). Experiments have since established the existence of such a mechanism as well as having emphasized greatly the importance of intraspecific competition in the regulation and control of rodent populations. We now believe that competition is the primary factor regulating and controlling the growth and decline of rodent populations and that nutritional or environmental deficiencies affect populations mainly by increasing competition as had been suggested by Davis (1949) and later developed in greater detail (Christian 1957).

POPULATION CHARACTERISTICS AND FORCES

No attempt to describe the various characteristics of rat populations will be made here, as the subject has been thoroughly reviewed elsewhere (Davis, 1953). The same applies to the forces affecting population growth, namely: mortality, reproduction and movements. Suffice it to say that any factor operating to decrease reproduction and/or increase mortality will reduce the

size of the population, and conversely, any factor increasing reproduction and/or decreasing mortality will produce an increase in population size. Immigration in a sense may be considered to parallel increased reproduction and emmigration increased mortality. The logical way to control rodent populations is therefore to find a method of increasing mortality and decreasing reproduction by utilizing factors in the life-equation of the given animals. We shall see that social competition, varying in intensity with the size of a population, produces physiological responses which result in precisely these effects on reproduction and mortality. Therefore competition, as part of sociopsychological-physiological feed-back system, may be used as a means of regulating and limiting population growth.

THE THEORY AND THE EXPERIMENTAL EVIDENCE

It is now well established that a wide variety of noxious stimuli produce a condition of "stress" in animals subjected to these stimuli (Selye, 1946). The "stress' manifests itself by eliciting increased activity of the anterior pituitary-adrenocortical system which is measurable by increases in adrenal weight and increased production of adrenocortical steroids (Sayers and Sayers, 1949; Nelson, 1956). The hypothalamus is probably an integral link between the higher centers of the central nervous system and the anterior pituitary (Harris, 1956). Our theory proposed that with increasing population size there would be increasing social pressures (competition) which would act as stimuli to the production of stress in the individuals of a population. The stress would be in some proportional relationship to population density and would therefore elicit a proportional response in the pituitary-adrenocortical system. It was also postulated that reproduction, growth and resistance to disease would decline in proportion to the increase in adrenocortical activity and therefore to population density (Christian, 1950, 1957). Presumably the sociopsychological pressures would act through the higher brain centers to stimulate the appropriate center in the hypothalamus which in turn would stimulate increased adrenocorticotrophin production and inhibit the production of growth and gonadotrophic hormones. It was therefore necessary to demonstrate a positive relationship between population density and the activity and size of the adrenal cortex and a negative relationship between population density and reproductive function. In order to establish that competition was purely social and always present and active in relation to density it was absolutely essential to eliminate competition for food, water and nest space (and harborage when appropriate). Therefore all experimental populations were liberally provided with food and water from several sources at all times and, where pertinent, nest space and harborage were provided in excess of their usage. The adrenal glands were weighed routinely and enough examined histologically to establish that weight changes were due primarily to changes in the amount of cortical tissue, specifically of the zona fasciculata. The weights of the thymus and preputial glands were taken for both sexes and the weights of the seminal vesicles and testes were also obtained for the males. The ovaries and uteri of all females were examined for pertinent reproductive data. (Christian, 1955 a, b, 1956).

Prior to initiating or during the course of our program there were a number of experiments conducted with mice in the laboratory which indicated a relationship between reproductive performance and population density (Crew and Mirskaia, 1931; Retzlaff, 1938; Andervont, 1944). There also have been several experiments suggesting that competitive social behaviour resulted in stress with a correspondingly increased adrenocortical activity. Barnett showed that the subordinate male rats in a group had larger adrenals with presumably a greater production of adrenocortical steroids than their dominan brethren (Barnett, 1955). He further noted that mortality in these animals was probably not related to fighting but rather to exhaustion or "shock", confirming our observations for mice (Christian, 1954). Clarke (1952) demonstrated an increase in adrenal weight, thymic involution, and splenic hypertrophy associated with placing alien voles in with a pair indigenous to the cage. Finally, Bullough showed that the adrenal cortices in grouped mice were larger than in isolated controls (1952). It is noteworthy, however, that none of these experiments were designed to show a relationship between progressive changes in population density and the adrenal cortex, a point essential to the theory which assigns the fundamental responsibility of controlling the growth of mammalian populations to density-dependent physiological responses. Our experiments were designed specifically to demonstrate such a relationship.

We first were able to show that when previously isolated male mice were placed together the weights of their adrenal glands a week later were

related to population density, apparently to the logarithm 10 of the population size (Christian, 1955 a, b). It appeared that the weights of the adrenals decreased from preceding levels after a certain level of population was reached, but this anomaly was later explained by demonstrating a marked depletion of the intracellular cortical lipids even though the number of cells had actually increased (Christian, Unpbl.). Paralleling the progressive increase in adrenal weight with progressive increases in population size, there was an inverse relationship between the weights and activity of the reproductive organs. These same relationships were shown to exist in freely growing populations of wild house mice (Christian, 1956). The latter experiments additionally demonstrated that female mice were affected similarly to the males, but to a quantitatively smaller extent. Birthrates and infant survival rates declined linearly with the logarithm 10 of the increasing population size. The younger animals (and presumably subordinate) were more severely affected than the larger and older animals. There was a marked delay with respect to body weight in the attainment of reproductive maturity, as was shown by the development of the reproductive organs and the onset of spermatogenesis in males and pregnancy in the females. The effects on reproduction and the adrenal glands were probably greater than indicated with respect to chronological age as there was probably a suppression of growth and therefore of body weight. Observations during the course of these experiments and at autopsy suggested that the deleterious direct effects of increased population density on the development and survival of the young were augmented by diminished lactation. There were indications that lactation had been suppressed in the females along with the other reproductive functions. Chitty (1955) found this to be the case with voles in experimental populations, and we were able to confirm his results using albino house mice (Christian and LeMunyan, Unpbl.). We found in addition that the effects of diminished lactation attendant on crowding suppressed the growth of suckling infants in relation to litter size (the larger the litter size, the more pronounced the effect). These effects were also manifest for at least two generations of progeny. Following the demonstration of these phenomena in the laboratory we were able to show that the adrenal glands of wild Norway rats similarly responded to changes in population density, in spite of an abundance of food and harborage (Christian and Davis, 1956, Fig. 1). A relationship between the prevalence of pregnancy and population status in rats had been demonstrated earlier (Davis, 1953). In another experiment we were able to reduce adrenal weight appreciably by reducing the density of three populations of rats (Christian and Davis, 1955, Fig. 2). In another experiment a close relationship between population on size and adrenal weight was shown in a population of farm rats samples monthly for approximately three years (Christian, 1954 and Unpbl.). Finally, we demonstrated a relationship between adrenal weight and social rank in mice with the dominant animals having the smallest adrenals (Davis and Christian, 1957).

The results of other investigators, using populations of house mice or voles in the laboratory or voles in the wild, fit the theory and coincide with our results (Brown, 1953; Frank, 1953; Strecker and Emlen, 1953; Clarke, 1955; Louch, 1956; Kalela, 1957). The combined results of these experiments indicate and emphasize the fundamental role of social competition in the regulation of rodent populations. Controlling rat populations by increasing competition (Davis, 1951) therefore has a sound basis in biological fact.

THE PRINCIPLE OF CONTROLLING RAT POPULATIONS

It has been recognized for some time that general sanitation is an effective means of keeping populations of rats under control and has been a highly successful procedure in urban areas (Davis, 1951). It has been demonstrated repeatedly that a reduction in the environmental capacity results in a proportionately much greater decrease in the number of rats that one would have predicted, indicating that a change in the environment in a direction unfavorable to the continued support of rat population was not directly responsible for reducing the populations. Sanitation evidently acted as a means of increasing competition which was in turn directly responsible for the reductions in populations size. Sanitation of this sort is frequently difficult to carry out, particularly in rural areas (Barnett, 1952), therefore it is logical to seek other means of increasing competition. The results of early experiments suggested that the introduction of alien rats into a population might be an effective means of increasing competition (Davis, 1953). Subsequently a series of experiments designed specifically to explore such effects were carried out (Davis and Christian, 1956). These experiments were conducted with increasing and stationary

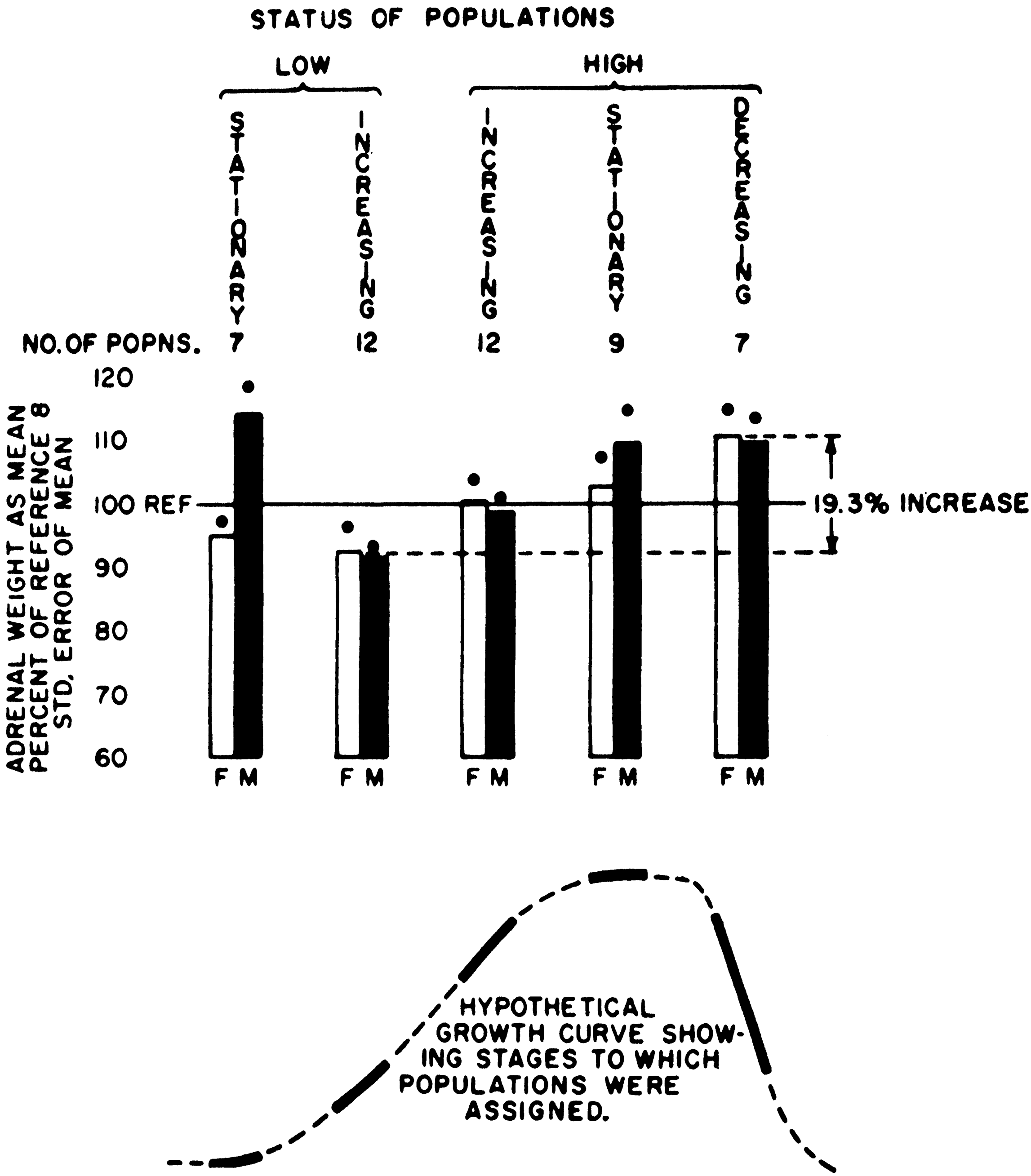

Fig. 1.—The relationship between the level of population and adrenal weight for populations of urban Norway rats. Each population was assigned to one of the five separate categories into which an hypothetical growth curve was divided. The means of the mean values of each population for each sex is given with its standard error. The number of populations in the sample for each category of population development is given.

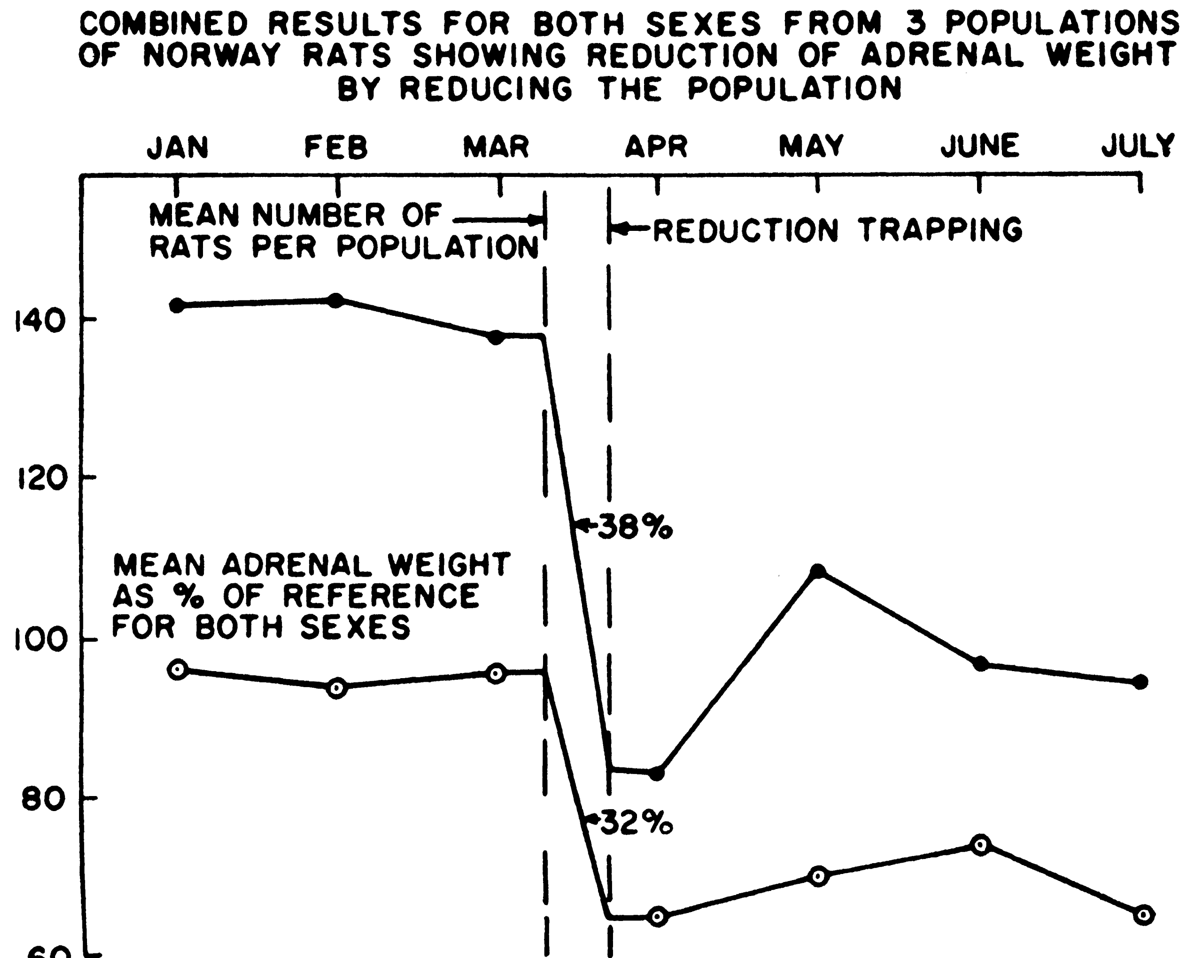

Fig. 2.—The pronounced reduction in adrenal weight achieved by artificially reducing the populations. Three populations were used in this experiment; all were at relatively high levels initially. The sexes have been combined, as there were no appreciable differences between them on the responses of their adrenal glands.

populations of Norway rats (Fig. 3). In each case a number of rats of one sex was removed from the population and subsequently replaced either by an approximately equal number of the same sex or by a considerably greater number than was removed. When the removed rats were only replaced, increasing populations ceased growing and stationary populations remained essentially the same (Fig. 3). However, when a much greater number of rats was added than were removed, stationary populations declined sharply from the original level. The latter procedure was not followed for increasing populations. These results show that the introduction of strange rats of either sex, even without increasing the population size, has profound effects on population growth. These effects can have been due to social competition only, as the populations were well below the capacities of the areas. The marked reduction of stationary populations to well below the environmental capacity effected by increasing the population with alien rats leads to the same conclusions. It is apparent that sanitation is not the only method of increasing competition and thereby reducing population size. Any means which can be found to increase the competition in a given population apparently can be used as a means of control. The above results serve to emphasize the self-defeating aspects of trapping and poisoning campaigns

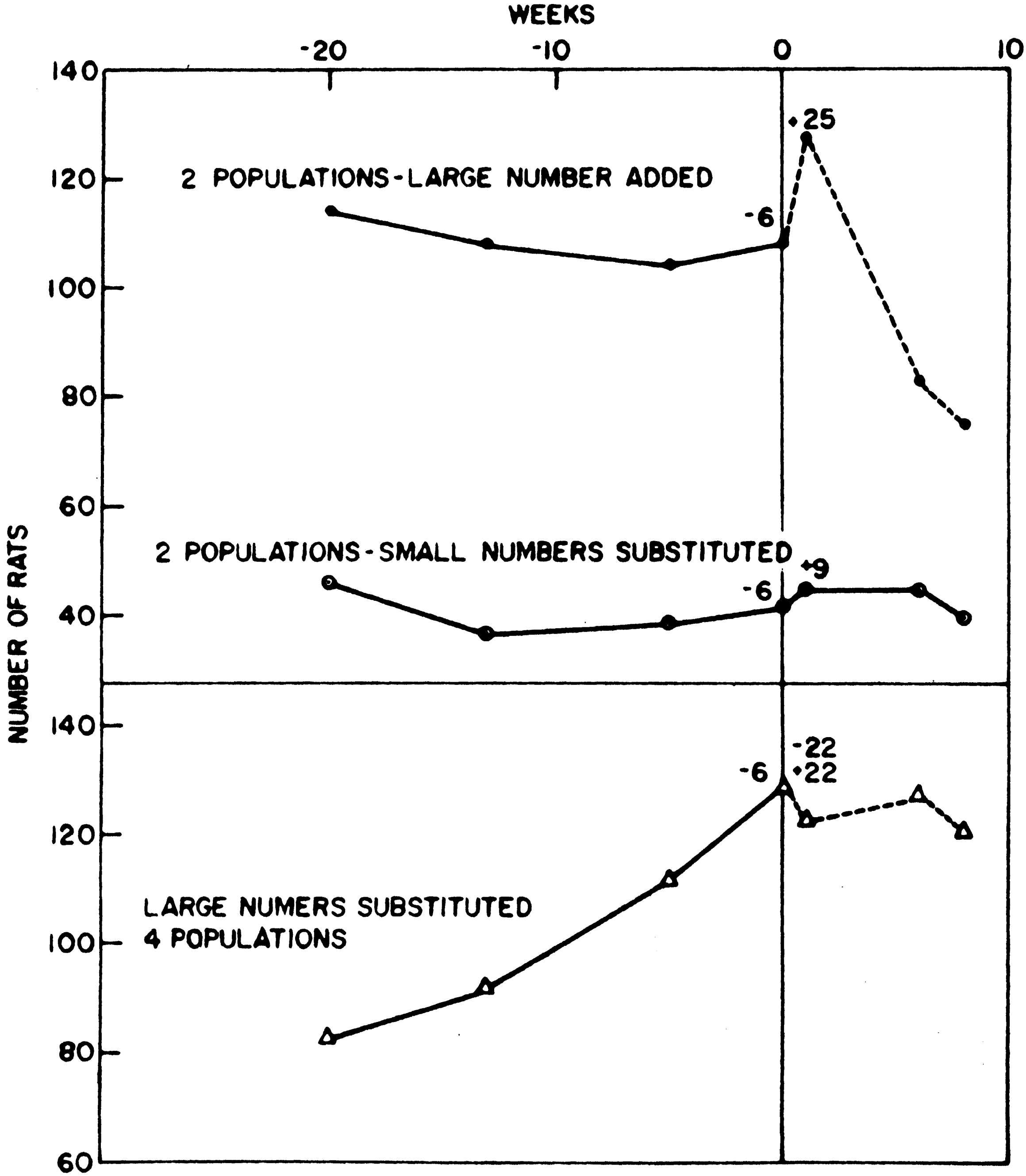

Fig. 3—The effects of introducing various numbers of alien rats into existing populations. The introduction of a large number of rats into 2 stationary populations resluted in a marked decline in the numbers of rats from the initial levels. Removing small numbers of rats from 2 stationary populations and substituting aliens for these had little effect on the populations. Substituting large numbers of alien rats for native rats in 2 rapidly increasing populations resulted in a cessation of the growth of the populations.

(or any other reduction of populations not using the intrinsic mechanisms of population growth) unless they are on a sustained basis with great intensity or by utilizing involved techniques, such as prebaiting (Barnett, 1952), with a high cost in time and effort. Even then these efforts may fail, as has been cited earlier.

PRINCIPLES OF CONTROL AND SUMMARY

The two primary forces affecting the growth of populations are mortality and reproduction. Increasing mortality alone, at least of the mature population, usually has little effect on the population since it stimulates increased reproduction as well as an increased survival rate of those individuals which do not succumb. Trapping, poisoning, and disease, therefore are at best usually only temporary expedients in controlling rodent populations. It is true that with an extremely intensive and sustained trapping program control can be achieved, but the amount of effort required will usually be prohibitive. It is apparent therefore that in order to have an effective program of rodent control we must use some means of significantly curtailing reproduction and/or infant survival. If such a means also increases adult mortality, we are that much better off. We have suggested that an effective means of achieving decreased reproduction and increased mortality of adult and infant rats and mice is to increase competition. This suggestion is supported by a variety of experimental evidence from the laboratory and the field. At the present time we are unaware of any other method of successfully altering reproduction and particularly with such prolonged effects. We have also pointed out that the means of increasing competition will have to be determined for each particular situation. This method of rodent control is based on our knowledge of the biology of rodent populations and its application will still further depend on the utilization of biological facts and principles. Failure to recognize and utilize these biological principles in the long run will result in a failure to achieve successful rodent control.

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The opinions or assertions contained herein are the private ones of the writer and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large.

DISCUSSION

R.L. STRECKER: Actual numbers are not necessarily significant in terms of peak populations and their pressures. The important point is the amount of stress, regardless of size.

J.J. CHRISTIAN: Agreed. It depends on aggressiveness, physiological states, etc.

R.L. STRECKER: What is the explanation for population bursts?

J.J. CHRISTIAN: I know of no explanation as yet.

J.R. AUDY: Does it depend on the number of encounters?

J.J. CHRISTIAN: I do not think so. It depends on physiological states.

L.E. ROZEBOOM: Would not poisoning have the same effect as predation in bringing down population pressures to the point where survivors would not experience the stress phenomena and so constitute a healthier population?

J.J. CHRISTIAN: Essentially, yes.

A.G. SEARLE: Is the work done mostly on *R. norvegicus*?

J.J. CHRISTIAN: Mostly on *Mus musculus*, also other rats, squirrels, and now on marmots.

J.L. HARRISON: I call attention to Twitty's work on caged animals, where socially inferior animals showed swelling and slipping of intervertebral discs. Also *R. Jalorensis*, pest of oil palms occurring in large numbers show smaller litter size, lower pregnancy rates and smaller skull length than those in the scrub where they are part of a larger community.

J.L. HARRISON: What is known about stress within species and between species?

J.J. CHRISTIAN: Not much is known yet.

A.R. MEAD: What is the effect of introduction of a species when the indigenous species is in high stress state?

J.J. CHRISTIAN: When one reduces a dominant species experimentally, an inferior species will rise in population.

R.L. STRECKER: Then it is a better sanitary practice to reduce the capacity of the habitat to support a population and leave the population undisturbed rather than reduce the population, as by trapping, at the same time.

J.J. CHRISTIAN: This is the practice in Baltimore.

H. TRAPIDO: How quickly do these reduced populations recover?

J.J. CHRISTIAN: For *R. norvegicus*, 6 months. In control practice, a population reduced 50% comes back rapidly.

H. TRAPIDO: What is the definition of this stress to which you refer?

J.J. CHRISTIAN: Actually we do not define what stress is except in terms of the animals response to it.

R.L. STRECKER: Stress is anything which requires the animal to adapt. Life is all stress. When some new condition occurs, stress responses occur.

H. TRAPIDO: Then why does poisoning not affect the population and elicit stress response?

J.J. CHRISTIAN: Those to which the dose is not lethal are stronger and healthier individuals.

J.L. HARRISON: Only individuals, not populations, learn about poison and avoid it. Then it is no longer a serious stress factor to them.

J.R. AUDY: An apparent paradox is observed: animal most able to rise in great numbers seem the most high strung.

J.J. CHRISTIAN: We must learn what comprises competitive situations within populations. There is much variability in the number of fights and other behavioral factors.

J.R. AUDY: Variation in aggressiveness seems responsible for occurrence of large numbers.

J.L. HARRISON: The "bad tempered" animals are the successful ones. They cause the stress to others.

J.J. CHRISTIAN: Dominant animals certainly are the most secure.

I. MCT. COWAN: It seems that this general topic would lead to species adapted to "slum conditions." This seems to have happened in rats, mice, and man.

J.J. CHRISTIAN: Parallel to this, with *Peromyscus* we couldn't get over 12 animals to live together, while *Mus musculus* over 100 live together. Reserpine (a tranquilizer) helps raise population size of *Peromyscus*.

OBSERVATIONS ON THE RAT INFESTATION OF COTABATO, THE PHILIPPINES

R.J. CLARK

FAO Technical Assistance Expert on Rodent Control, Manila, Philippines.†

INTRODUCTION

In the Philippines, there are more than thirty species of rodents. Because of their numbers and habits several are major pests. This paper concerns one species of rat which is widespread in the islands but which has been most intensively studied in the provinces of Cotabato where it is a serious agricultural pest. Data presented here were collected while the author was serving with the Philippine Government as a Technical Assistance Expert in Rodent Control for the Food and Agriculture Organisation of the United Nations from May, 1956 to May, 1957.

Cotabato is the largest of the ten provinces in the island of Mindanao with an area of 2,296, 790 hectares. In the large central lowland plain the main crops are rice and maize (*Zea mais*). These have suffered severely from the depredations of rodents and, after an outbreak destroyed a large proportion of crops in 1953-4 and subsequently, organised rodent control was begun by the Philippine Government.

PROBLEM

In Cotabato, the species causing most concern at present has been identified, from specimens sent to E. Hill of the British Museum (Natural History), as *Rattus argentiventer*. Until 1954 no studies of this animal had been made in Mindanao. Between then and 1956 a number of laboratory examinations made by P. Soriano, Bureau of Plant Industry, Manila, showed that *R. argentiventer* could be killed by the rodenticides: sodium fluoracetate, arsenious oxide, thallium sulphate, warfarin, tomorin and pival. At the same time, field and laboratory studies by N.C. Rosell and J.P. Sumañgil, also of the Bureau of Plant Industry, disclosed that these rats had a breeding season from July to December, delivered an average of 4 litters per breeding season with about 6 young per litter.

The main problem was to increase the efficiency of control methods. To do this it was necessary to study the response of the rats to various techniques in the field and for this purpose a number of experiments were conducted in the wet season during the latter half of 1956 and in the dry season during the early part of 1957.

Although the field experiments were chosen primarily to provide a basis on which to adapt and recommend methods of control suited to local conditions, they also indicate in some respects how the behaviour of field rats in Cotabato compares with that of similar rodents elsewhere.

EXPERIMENTAL METHODS AND DATA

Spacing of baits—The laying of baits in an economic manner precludes spending much time examining the ground for all signs of the presence of rats. This is because the environment includes thick undergrowth of grasses, often in marshy ground where progress is hampered and the rat traces hidden from casual observation. Thus, although as much time as possible should be given to siting baits in relation to the rat traces present, it is necessary to know what minimum density of baiting sites will supply a rat population irrespective of the position of rat traces.

The amount of bait taken by rats from containers spaced at various intervals was used to compare the effectiveness of different densities of baiting sites. At first, baits were placed 20 metres apart. Twenty-five containers were laid: five in each of five rows. Containers were tubes, open at each end with a minimum internal diameter of 75 mm., made by cutting nodes of bamboo. Vegetation covering the baited area was mixed. Some of the containers were in patches of growing rice and maize or near a banana clump, and a few were on ground which had been cleared prior to planting but most were in uncultivated patches. The uncultivated sections included forest trees with undergrowth as well as areas of grasses, mainly *Saccharum spontaneum* (2 m. high) and *Imperata cylindrica* (up to 1 m. high) but also some short grass. Surplus quantities of bait were used at each of the 25 sites, uneaten bait was weighed each day and

† U.K. Ministry of Agriculture, Fisheries, and Food, Infestation Division, acting as Food and Agricultural Organization technical adviser in the Philippines.

fresh weighed baits replaced. The total nightly consumption of the maize meal increased from 1.5 g. on the first night to 1,120 g. on the twelfth night. On the two following nights 932 g. and 1,190 g. were eaten. The mean peak consumption was therefore recorded as 1,090 g. For three days following this, baiting sites were added so that baits were only 10 m. apart. From the nine rows with nine containers each, bait consumption was 1,570 g. on the fifteenth night and 1,760 g. on each of the two following nights. The mean consumption of 1,700 g. suggested that spacing of baits 20 m. apart did not sample the population nearly as well as baits at 10 m. distances.

In another experiment a similar procedure was adopted but in reverse. That is, baits were laid at 10 m. intervals and, after measuring the mean peak consumption, a 20 m. interval was used and consumption compared. With a 10 m. spacing in varied vegetation as before, the mean peak consumption was 740 g. from the 81 baiting sites. This figure was obtained from the results of the 10th, 12th and 13th nights after baiting commenced, those of 11th night were discarded as many of the baiting sites were flooded after unusually heavy rain. Immediately the number of baiting sites was reduced, consumption fell to 412 g. and in five consecutive nights, varied between this and 370 g. the mean consumption being 400 g. The 25 baits were not sampling the area effectively. They were then increased to 36 sites spaced 15 m. apart. These were at different positions from any of the previous bait sites, and the area covered was necessarily slightly smaller. Consumption slowly and erratically rose from a low level to overtake that achieved from the 25 baits. Possibly the long conditioning to feed at the previous bait sites prevented the usual steady rise to a maximum amount of bait eaten each night. The mean peak consumption, from days 13, 14 and 15 after baiting commenced at the new sites was 470 g. These results supported the belief that baiting sites as far apart as 15 or 20 m. would not feed all the rats. Attempts to control rats by poison baiting with a density of less than 100 bait sites per hectare could therefore be expected to be unreliable.

In these tests it was assumed that the disappearance of bait from the containers was entirely due to rats feeding. There was evidence, such as the presence of rat faeces on the surplus food, the gnawing of containers, the sight and sound of rats visiting baits at night, the clearer demarcation of runs leading to the baits; that rats were responsible for much of the bait consumption but it was also evident that ants and perhaps many insects could attack the baits. However, later use of rodenticides at these plots, followed by daily measurement of weighed baits showed that consumption could be reduced to between zero and 50 g. per day, with consequent disappearance of rat traces and without evidence of change in insect activity. Other investigations also indicated that insects did not remove sufficient bait to affect seriously results obtained. In some later experiments there were times when monkeys and wild pigs interfered with baiting operations but their activities were obvious when they occurred and repetition could usually be prevented, so that few experiments were vitiated by their interference.

The initial tests did not indicate whether all rats within the areas fed from baits even at 10 m. intervals, nor what proportion of their diet the baits provided. Simple, open-plot experiments could not answer these questions; but enclosed areas provided indication later, that it was not necessary to site baits as close as 5 m. apart.

Consumption of baits—Feeding from containers did not commence freely as soon as baits were inserted. In areas where no previous baiting had occurred, or where containers were moved from established positions, the amount of bait taken each night was small at first but increased each night to a maximum. In twenty different baiting trials over a period of ten months it always took time to reach maximum consumption, sometimes a few days, sometimes several weeks. The delay in reaching a maximum could be due to one or more of several factors: time taken for rats living near the baits to locate them, initial avoidance by rats which do find the baits, or increasing numbers of rats from a distance finding their way to the area. Whatever its cause, it was clear that immediate application of poison baits in containers could not kill more than a small proportion of the rats living in or near the area.

In an attempt to obtain information about the relative densities of infestation in various habitats, using the amounts of baits taken as an index; it was necessary, not only to continue the baiting long enough to record a maximum figure, but also to standardise the baiting technique. After a little experience a standard experimental procedure was adopted of providing weighed baits in bamboo containers at 100 baiting sites set out in ten lines spaced approximately 10 m.

apart, so covering a plot of one hectare. Records were made of bait taken at individual sites as well as total consumption on the plots in order to examine the relationship between environment and feeding. The mean peak consumption using rice binlid (rice shorts) as bait provided a measure of the feeding capacity of rats by which the level of infestation on different patches of ground might be compared. The mean peak consumption varied from 1.5 kg. to more than 17 kg. in various, previously untreated, areas. There was no close relation between the presence of crops, water courses, or number of observable rat traces such as feces, footprints, runways, holes, collections of cut stems, or damaged plants; and the level of infestation. A fairly high level of infestation was present throughout the area with patches very heavily infested. In these patches there was usually good ground cover, either of crops or wild grasses, where rats could run without being seen.

The attachment of rats to covering vegetation was noticeable where a baited plot included various types of cover: for example, forest, short grass, taller grasses and sedges such as *Echinchloa*, *Imperata*, *Polygonum*, *Scirpus* and *Saccharum*. Much more was eaten from sites among the latter plants than the former. Those sites in a plot favored by the rats were consistently used.

When, in the course of providing surplus quantities of fresh bait at each site, the capacity of a bait container was liable to be exceeded, an extra one or more containers, was placed alongside the original at the same baiting site. Each bamboo tube could hold up to 100 grams of rice binlid without suffering too much loss from spillage, while the rats fed; but above this figure, and at lower figures for bulkier baits such as rice bran, extra containers were necessary. Sometimes the addition of a container was followed by a temporary drop in consumption of that baiting site, or a failure to increase the nightly consumption as rapidly as expected, but this effect disappeared within a day or two.

Field preference tests—The successful application of poison baiting techniques depends as much on the choice of baits as on the effectiveness of the poisons mixed with them. While such factors as availability, cost and ease of preparation influence the choice of baiting material, the most important factor is the acceptability to the species of rat causing the infestation. A number of preliminary cage tests were performed to compare some of the baits, but with rats under laboratory conditions preferences were affected by previous diet to a much greater extent that was the case under field conditions. In the field the following materials were tested for acceptability: rice bran, cornmeal, rice binlid, fresh and dried grated coconut, maize grains (dry and boiled) cassava flour, grated cassava root, fresh and dried shrimps.

For each preference test one pair of materials was chosen and an infested plot of ground selected. Usually twenty baiting sites were employed in two lines of ten. The lines were ten metres apart, and at ten metre intervals in each line, bait containers were positioned close to any rat traces which might be found within a few metres of the marker. Sketch maps of the bait layouts showing type of vegetation and compass directions were prepared to facilitate location of baits in the undergrowth and to record consumption in relation to environment. At each numbered baiting site two containers marked A and B, were placed side by side to hold the two baits. Beginning with 10 gram quantities of each, renewed supplies of bait were given each day, the quantities being trebled each time more than half the previous day's supply was eaten. Uneaten residues were weighed to enable the amounts taken to be calculated. To overcome possible effects due to one container being in a more advantageous position than the other, they were interchanged each day. Thus, if a rat approaching a site from one side, met bait A one night: it would meet bait B first on the following night.

Comparisons of the various baits are illustrated in the accompanying graphs.

Bait containers—To prevent bait being washed away by rain, and to reduce the possibility of poison being eaten by domestic animals when these are present, containers are used at baiting sites. In one test, three types of containers were compared. Type A was a bamboo tube about 8 cm. internal diameter and one internode in length, open at each end which was cut slantwise to provide an overhang. Type B was of similar bamboo but one node was left intact so that one end was blocked. Type C was tent-shaped made of a wooden frame thatched with leaves and provided with a shelf just above ground level. Nine rows of nine containers approximately ten metres apart were set up. The site was chosen for its homogeneity of vegetation. Three of each type of container were used in each row and their positions in the row were randomly selected. The ground was uncultivated, covered with grassy

vegetation and, at the time of the test, waterlogged. Cornmeal was used as a bait and its consumption at each baiting site measured. After a two week period, during which the total amount eaten increased from 50 grams per day to 400 grams, the results for the following six days from each type of container are summarised in the table.

	August.			September.		
Date	28	29	30	31	1	2
Grams taken from						
Type A	332	268	250	179	278	254
Type B	16	36	21	10	14	35
Type C	102	274	201	111	123	171

The superiority of types A and C over the containers with one end blocked is obvious. There may be an advantage in type A compared with the tent-shaped container, type C, but there is no statistical significance in the difference between results from A and C in this experiment. Type A is certainly easier to prepare and transport when suitable bamboo is obtainable. When it is not, a simple inverted v-shaped or u-shaped metal cover made from a rectangle 30 cm. × 20 cm. is satisfactory.

Comparison between metal covers and bamboo tubes was made by a test analogous to a bait preference test. At each of twenty baiting sites, a pair of containers: one metal, one bamboo, was used: equal quantities of rice bran were placed in each and renewed daily. Almost equal amounts were eaten daily from these two type of containers.

Efficacy of Poisons—Preliminary cage tests had shown that various rodenticides when administered with food were capable of killing *R. robiginosus*. Field trials were chiefly concerned with measuring the effectiveness of methods of poison baiting. The LD_{50} for none of the rodenticides for this species is known, and even if they were there would still remain the task of relating lethal dose to palatability in order to determine the optimum concentration for field work. It would have taken considerable time to collect the information necessary for this to be done. A quicker initial approach was to use various concentrations of the different poisons in a series of standard field trials and to estimate the proportion of survivors from each trial.

Assessment of the effectiveness of any type of treatment in the field resolves itself into obtaining a measure of the population before and after treatment. This need not be an absolute measure but it must be done in such a way that comparison of the two results reflects fairly accurately the effect of the treatment. Marking, and recapture methods can be used to estimate rat populations but the process is slow and problems due to avoidance of capture can occur. Estimates can be based on killing and counting the rats in specified areas, carrying out control measures in other similar areas, and then killing any survivors in the same way as for the initial count. A very large number of areas are required if a reasonably accurate assessment is wanted. The types of environment usually encountered provided much too dense a cover for counts of live rats seen to be of any value as an index of the population, nor were any of the rat traces very useful for this purpose: some were difficult to find, some e.g. footprints were much affected by the amount and time of incidence of rain, this species makes relatively few holes especially in waterlogged ground where its nests are often above ground, hidden among grasses, faeces disintegrated rapidly and the use of standard dropping boards for counting these did not seem satisfactory.

The method of estimating relative populations before and after treatments which was used, was based on the census baiting method of Chitty and Southern and Doty. At first, these estimates of feeding capacity and the treatments to be tested were carried out on open experimental plots but eventually it was found necessary to use enclosed plots.

Open plot technique—A standard sized plot, 100 metres square, was used and within this one hectare, 100 baiting sites were distributed. At these sites a bait, different from the one to be employed in the treatment, was used to measure the daily consumption by rats visiting the baiting sites. The amount of bait consumed when the maximum was reached and on two succeeding nights was averaged to give a pre-treatment census figure. The treatment was then commenced using different baiting sites. After the treatment, census baiting was again performed using the same sites and bait as before the treatment. Thus a post-treatment census figure was obtained and the possibility of bait shyness or place shyness affecting the results was avoided.

This method can give a satisfactory estimate of the effectiveness of a treatment only when certain conditions are fulfilled:

1. A large proportion of the rat population must take all or most of its food from the baits.

2. There must be the same relation before and after the treatment between feeding and the numbers of animals present.

3. Movement of rats to and from the area involved must not be on such a scale and so undirectional as to affect the estimate.

4. The baits must be free from substantial attack by other animals.

The first and last of these conditions were fulfilled. For the second condition there was no indication of any marked change of behaviour on the part of survivors that would affect the results; it was probably fulfilled but there can be no certainty of this. Regarding the third condition: movement of rats into the baited areas frequently occurred with the open type of experimental plot first used. It was impossible to overcome this difficulty by treating simultaneously the whole of an infestation as this involved at least several thousand hectares. Bait barriers, sometimes with rows of baits only two metres apart, around the periphery of experimental plots; could not be relied upon to prevent the influx of rats during a baiting period. Thus, using the open plot technique, the estimated success of various poison treatments was often low; the measurement representing a combination of survival and inflow of rats after the treatment. In a few cases the post census figure was nil or almost so; that is, invasion of the plot after treatment obviously did not occur and the prebaiting and poisoning was extremely effective, but usually, varied results were obtained.

So far as these are measures of the effect of applying treatments to small patches of a large infested area they are worth recording, but they do not represent the effectiveness of the poisons:-

Method of Treatment Prebait used. Poison used.	Pre-census figure grams	Post census figure grams	Estimated Success
1. Maize meal. 4% Zinc phosphide. (Initial treatment of plot)	1,700	740	56%
2. Rice bran. 5% arsenious oxide (Second treatment of previous plot)	740	40	93%
3. Rice bran. 15% arsenious oxide (Initial treatment)	1,000	410	59%
4. Maize meal. 10% arsenious oxide (Initial treatment 7 days pre-baiting)	2,300	32	99%
5. Maize meal. 15% arsenious oxide (Initial treatment 7 days pre-baiting adjacent to previous plot)	2,200	38	98%
6. Rice binlid. 1.2% thallium sulphate (Initial treatment)	390	240	38%
7. Rice binlid. 0.4% thallium sulphate (Initial treatment)	430	180	58%
8. Rice bran. 10% arsenious oxide (Initial treatment)	6,400	1,900	70%
9. Sodium fluoracetate (Air dispersal of grain soaked in solution of rodenticide-direct poison)	7,930	1,640	79%

Enclosed Plots To determine to what extent the increase in consumption of baits each night was due to inflow of rats to a baited area, an experimental plot was enclosed by a metal barrier. The barrier was formed of flat sheets of galvanised iron, each 8 feet long and 3 feet high. The ends of each sheet were bent at right angles to form flanges which were bolted together on the inside of the barrier. The sheets were embedded 3 inches in dry ground or submerged to that extent in water in swampy ground. A square area of one hectare was enclosed. Within the enclosure bait consumption at 100 sites was measured.

The total amount of bait eaten per night rose from 240 grams to 440 grams in the first week and on the seventh night nine of the baits were completely eaten in spite of putting down increasing quantities. Baiting was then discontinued, from December 21st to January 2nd. With the recommencement of baiting 840 grams were eaten the first night, 620 grams the second night. After that the consumption fluctuated between 570 and 890 grams per night during a twelve day period, with daily fluctuations between 30 and 120 grams. Thus there was a process of conditioning occurring. Moreover, the practice of taking only a little food from containers at

first and increasing the consumption each night was not repeated after the twelve day gap in baiting: the rats retained their conditioning. After weighing and renewing bait on 14th January, one side of the barrier was removed and on each of the three following days another side was removed. Results were striking. 1,100 grams of bait were eaten the night after removing the first side, and 2,000 grams, 3,100 grams and 4,500 grams on succeeding nights. It was evident that a large number of rats invaded this experimental plot as soon as the barrier was removed and, knowing that this activity could occur, it was possible to understand better the results of some of the open plot experiments especially those where, after a period of two or three weeks, consumption had risen to more than 5 kg. per night and in one case more than 18 kg. without reaching a maximum figure.

Enclosure of areas permitted a more satisfactory estimate of the efficacy of poisons. The barrier sheets were erected to enclose a square with a side of 67 metres and with partitions dividing the square into four equal compartments. The site chosen had a homogeneous cover of Imperata. Twenty five baiting sites were usually used in each compartment; the sites were approximately 6 metres apart but positions used for treatments differed from those used in testing the effect of treatments. Water was placed in small troughs at the corners of the compartments in dry weather, as the enclosed rats were cut off from a ditch, which would normally have been accessible. During experimental periods, management of the enclosure included inspection of the barrier for attempted burrowing and clearing of weeds from either side of the metal. Only once did burrowing under the enclosure between the inside and outside occur. In the compartment affected, consumption of bait rose sharply: indicating that more animals entered the compartment than left. The rats initially enclosed were baited: within a week maximum consumption was reached in all compartments. Treatment with warfarin was completely successful in nine days, as shown in table:-

Compartment	A	B	C	D
Pre-treatment census figure	150g.	110g.	85g.	94g.
Treatment (Bait = rice binlid)	0.025% Warfarin	0.005% Warfarin	0.005% Warfarin	0.025% Warfarin
Post-treatment census figure	0	0	0	0

In open plot tests it was never possible to know exactly how many rats were present but with the enclosure free from rats, known numbers could be introduced to each compartment. Testing of poison baiting could therefore be carried out with greater accuracy and without the difficulties of interpretation due to influx of rats after the treatment. Ten rats were added to each compartment after the warfarin test. Eleven daily weighings provided a pre-treatment census figure. A prebait and poison treatment using thallium sulphate was then carried out followed by post-treatment weighings of bait.

Compartment	A	B	C	D
Pre-treatment census figure of 10 rats	160g.	160g.	170g.	results discarded burrow under barrier
Treatment (bait = rice binlid)	0.4% thallium sulphate	0.4% thallium sulphate	1.2% thallium sulphate	1.2% thallium sulphate
Post-treatment census figure	85g.	85g.	47g.	180g.

Thallium sulphate at these concentrations was evidently unsatisfactory.

Twenty rats were then added to the survivors in each compartment, prior to testing zinc phosphide treatments. The results are shown in table:—

Compartment	A	B	C	D
Pre-treatment census figure	340g.	370g.	450g.	510g.
Treatment (bait = rice binlid)	5% zinc phosphide	5% zinc phosphide	15% zinc phosphide	15% zinc phosphide
Post-treatment census figure	0	9g.	19g.	20g.

DISCUSSION

Although the data presented here do not permit many unequivocal statements to be made, and are quite insufficient to enable a complete conception of the general behaviour of the field rats in Cotabato to be gained, they do throw some light on those aspects of the behaviour of rodent pests which are of importance in devising control measures in this part of the Philippines.

The experimental results show that for poison baiting to be consistently successful attention has to be paid to the spacing of baiting sites, the type and concentration of poison and the type of bait. Direct poison baiting with acute poisons is less effective than the use of anticoagulants or

the placing of acute poisons after prolonged prebaiting, partly because the rats in the immediate neighbourhood of bait containers do not eat from them confidently at first and chiefly because, after a prolonged period of baiting, additional rats from surrounding areas find the baits. The foraging range of many of the rats probably exceeds 100 metres. At the same time, if baits are more than about 10 metres apart a proportion of the rats do not feed from them. It may be that social facilitation leads to rats crowding into a baited area and perhaps individual antagonism plays a part in a sparsely baited area but this could only be discovered by extensive behaviour study.

Of the poisons used, warfarin (0.005%), arsenious oxide (10%) and zinc phosphide (5%) are effective. Tomorin is similar in acceptability to warfarin. Preference tests, similar to those used to investigate baiting materials, were carried out with several commercial samples of warfarin and to compare 0.005% with 0.025% concentration. No significant differences in acceptability were observed. Thallium sulphate, at the concentrations tested, was less effective than other rodenticides. Aerial dispersal of grain soaked in sodium fluoracetate has a limited applicability in the Philippines. Only one open plot test of this method was made and movement of rats into the census baited plot after the treatment may have accounted for some of the 21% surviving the treatment. However, a very large area surrounding the test plot received poison bait at the same time: a total of 40 hectares were treated, so any rats moving into the test plot came from a depleted area. In addition to the main test plot two other portions of the 40 hectares were census baited, but only after the treatment. This was done chiefly to see if any appreciable difference occurred between survival in the treated 39 hectares and survival in the census baited and treated one hectare. Rat density was similar in all three areas after the air dispersal.

Among the various possible baiting materials some quite strong preferences were shown by the rats. Rice and rice binlid were the most acceptable of the baits tried. Rice bran, boiled maize and maize meal were reasonably acceptable. Coconut and cassava were of doubtful value. Freshwater shrimps were quite unsuitable: addition of these to a good bait such as rice binlid reduced the palatability.

Although a field preference test showed that rice binlid which had been used in the field and then stored again for several weeks was as acceptable to rats as unused rice binlid, none of the experiments reported here were done with re-used baits. For normal control measures of course, the use of surplus rice binlid from previous treatments is worth practising.

Despite the high humidity of the environment, it was not found necessary to incorporate mould inhibitors in baits as a regular procedure, although some tests with sodium dehydroacetate were carried out. There was some evidence that feeding habits were affected by rainfall in a manner similar to that found for Malayan rats by J.L. Harrison but this effect was often masked by the rising curve of consumption in the baiting trials.

It was not essential to equate bait consumption in the field with numbers of rats: experimental designs rested on comparisons of quantities, and accurate equating would be extremely difficult. Figures on consumption of bait by individual caged rats were, however, obtained and from two series of twenty rats in two laboratories a mean consumption of 10 grams (± 4) per day was obtained. It was expected that when known numbers of rats were introduced into enclosed plots in the field the mean consumption of bait would be smaller than this by an amount depending on the quantity of naturally occurring food which was taken. In fact, the bait taken in the enclosures was about 16 grams per rat per day. Unless higher figure obtained in the field was due to spillage, hoarding, waste or errors of measurement, it would seem that the rats were not only taking all or most of their nutriment in the form of bait but ate more than caged rats.

SUMMARY

Poison baiting techniques for the control of the local species of field rats are considered with special reference to types of bait and poison, and method of application.

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DISCUSSION

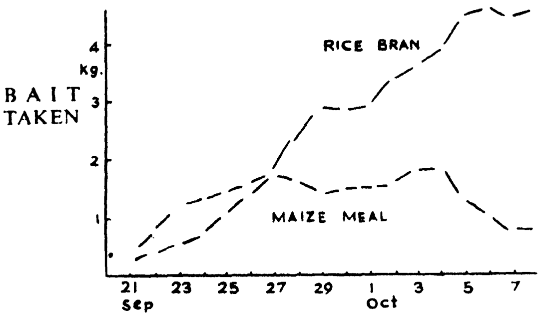
H. E. MCCLURE: It appears that the best bait is the one animals were accustomed to eating.

J. L. HARRISON: In Malaya, *R. argentiventer* in rice fields were best baited by grasshoppers, not rice. But some animals will not eat animal matter.

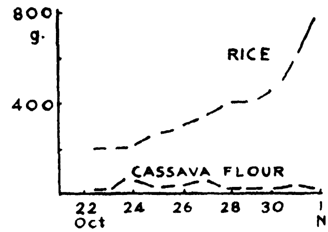
R. L. STRECKER: *R. rattus* take cacao, but *R. exulans* will not.

COMPARISON OF PAIRS OF BAITS

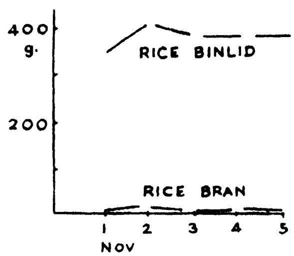
PREFERENCE TESTS



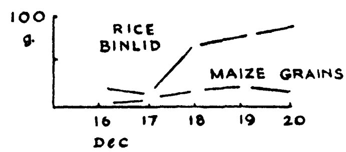
100 baiting sites in rice field.



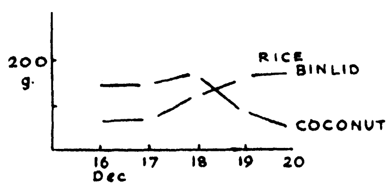
20 baiting sites, uncultivated ground.



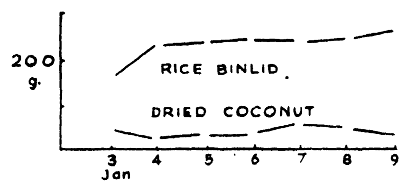
20 baiting sites near growing rice.



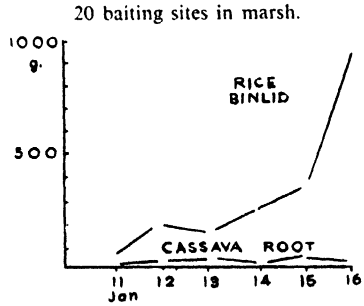
20 baiting sites in marsh.



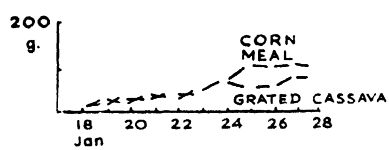
Coconut fresh at beginning of test.
No correction for moisture content
20 baiting sites in marsh.



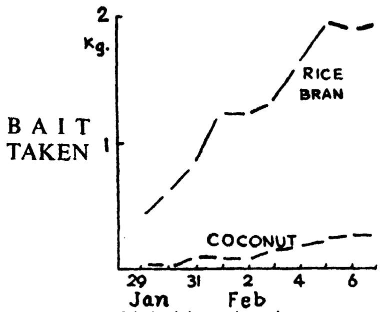
20 baiting sites as for fresh coconut.



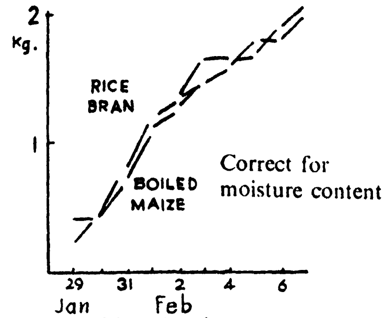
20 baiting sites near rice field after harvest.



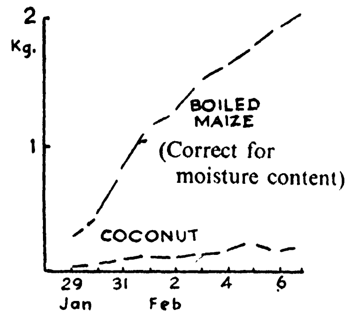
20 baiting sites among damaged growing corn (maize).



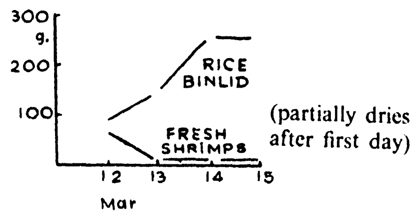
20 baiting sites in grasses.



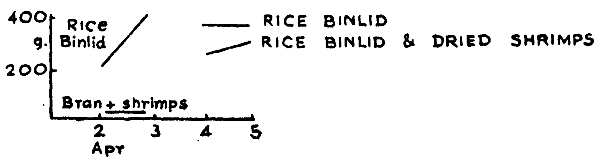
20 baiting sites in grasses.



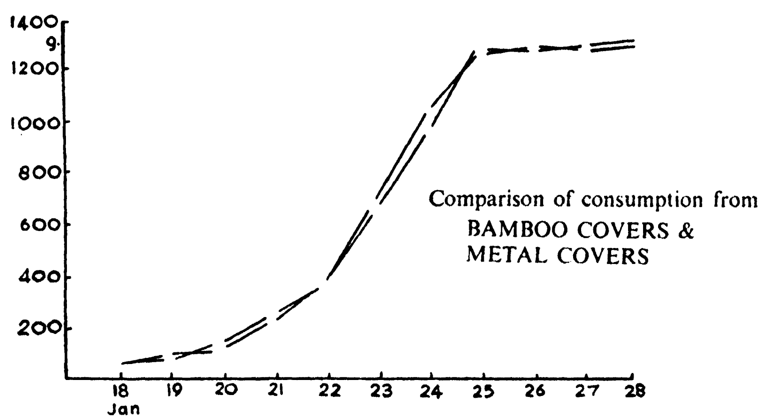
20 baiting sites in grasses.



20 baiting sites in grasses.



20 baiting sites near maize.



20 baiting sites among maize.

RECENT ECOLOGICAL STUDIES ON PLAGUE IN WILD RODENTS IN NORTHERN SAN MATEO COUNTY, CALIFORNIA

S.F. QUAN, L. KARTMAN, and F.M. PRINCE

U.S. Department of Health, Education, and Welfare, Public Health Service, Bureau of State Services, Communicable Disease Center, San Francisco Field Station, San Francisco, California, U.S.A.

Foci of sylvatic plague, similar to those studied in Kenya (Heisch *et al.*, 1953) and in Iran (Baltazard *et al.*, 1952) have been found during the last two decades in areas of northern San Mateo County, California within a few miles of the San Francisco city limits. This particular region is a narrow strip of land bounded by San Francisco Bay and the Pacific Ocean and characterized by low mountains, foothills, valleys, and flatlands. Much of the area is residential, either urban, or newly suburbanized, and portions contain industrial developments. The remainder is composed of undeveloped lands scattered in valleys, washes, and plateaus, with some farming and livestock enterprises.

According to Meyer (1934) plague was found in San Mateo County, California prior to 1934. Since that time, investigators from the California State Health Department (Unpublished and Anon, 1942) and the U.S. Public Health Service (Kartman *et al.*, 1958) have isolated *Pasteurella pestis* in northern San Mateo County at various times. In recent years the San Francisco Field Station, of the U.S. Public Health Service, has established several study areas in this region to investigate plague ecology. Figure 1 shows 5 of these study areas; areas A and C are adjacent to hog farms, area B is near a dairy, area D is close to a meat packing plant and a slaughter house, and area E is a wildlife refuge. The first 4 study areas contain both wild and domestic rodents, whereas the last contains only wild rodents. *P. pestis* has been isolated from fleas and rodent tissues from areas C and E.

The principal rodents in these study areas were the domestic rat, *Rattus norvegicus*, the California vole, *Microtus californicus*, the western harvest mouse, *Reithrodontomys megalotis*, the deer mouse, *Peromyscus maniculatus*, and the house mouse, *Mus musculus*. The principal fleas concerned were *Malaraeus telchinum*, *Catallagia wymanni*, *Hystrichopsylla linsdalei*, *Atyphloceras multidentatus*, *Opisodasys keeni nesiotus*, and *Nosopsyllus fasciatus*.

During 1953-1954 an intensive survey (Miles *et al.*, 1957) in the San Francisco region suggested that transfer of fleas between various rodent species was a significant feature of plague epizootiology here. For instance, *N. fasciatus* was found on 18 per cent of *M. californicus* and on 12 per cent of *P. maniculatus; M. telchinum* was taken on 5 per cent of Norway rats and these two flea species plus *C. wymanni* occurred on all the principal rodents trapped. *H. linsdalei* and *A. multidentatus* occurred with little discrimination on *M. californicus* and *P. maniculatus*, but were not found on rats.

Enzootic plague was found in persistent and delimited foci which went through periods of quiescence, when plague could not be demonstrated, to moderate incidence, and occasionally to exposive, highly transient epizootic incidents. Most of the plague findings were made in areas C and E (Fig. 1) where the situation was studied most intensively. The presence of *P. pestis* was indicated by animal inoculation of flea pools, by culture of individual fleas, and by culture of tissues from rodents found dead or moribund. The studies suggested that *M. californicus* was the chief plague reservoir since it was parasitized by the important vector fleas and by over 90 per cent of all species taken. The vectors *H. (Hystrichopsylla) linsdalei* and *M. telchinum* were the most prevalent species and were found to have relatively high natural plague infection rates during epizootics (i.e., 2 to 23 per cent, and 4 to 10 per cent respectively). Experimental studies showed that *H. linsdalei* is an efficient vector by individuals with a blocked proventriculus, whereas *M. telchinum* transmits primarily by mass mechanical means. Thus the former may act as the primary vector in this region, whereas the latter may be a secondary vector especially during epizootics.

Although plague was isolated from tissues of *M. californicus*, there was no evidence of a die-off of these rodent populations during an apparent epizootic period when the percentage of infected fleas increased. As a matter of fact, it was found that the incidence of plague increased during the spring season when the *Microtus* population increased from an average of 6 to 60 per trap night. These findings contrast with the picture of plague in colonial rodents where

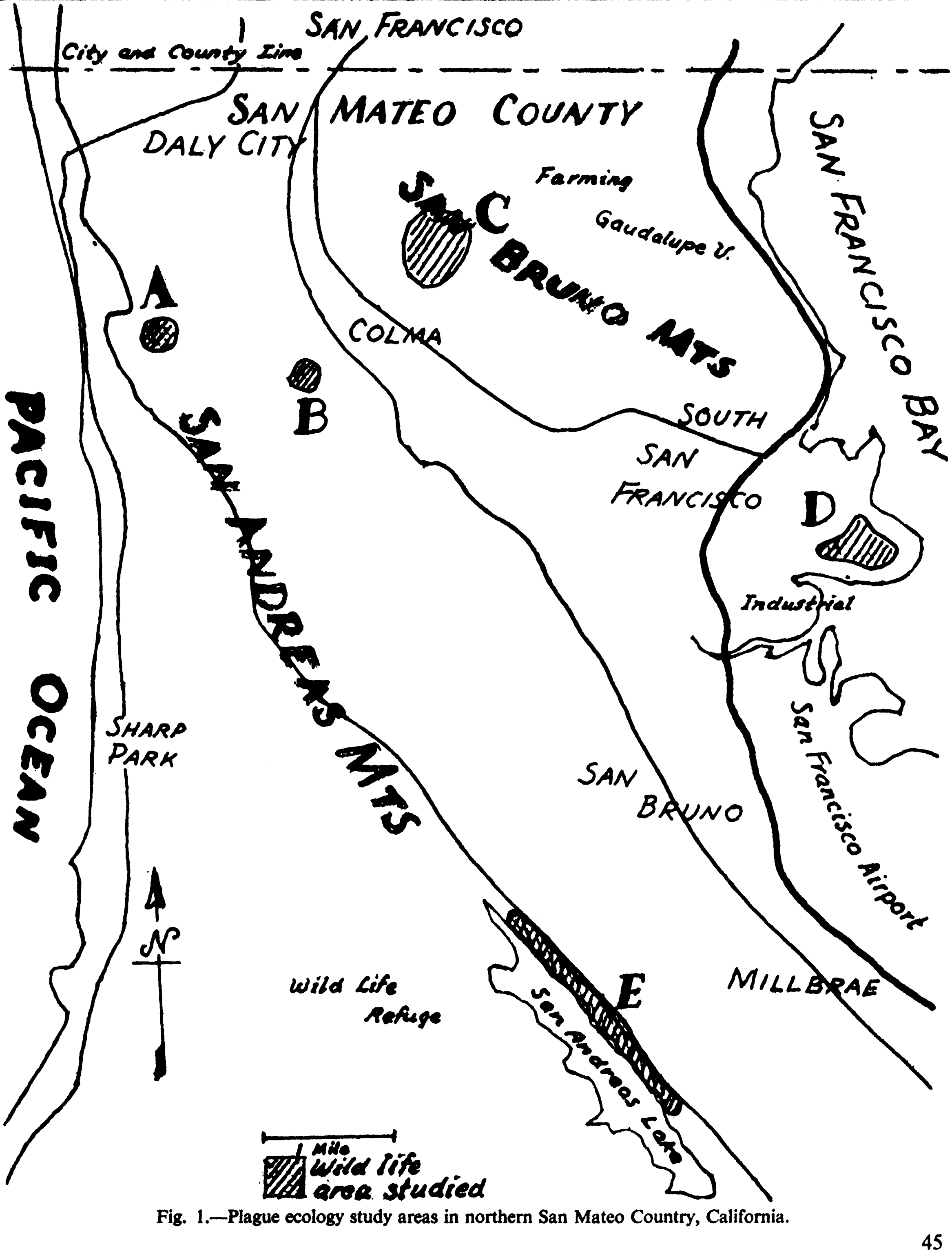


Fig. 1.—Plague ecology study areas in northern San Mateo Country, California.

whole "towns" of prairie dogs or colonies of ground squirrels have been decimated (Byington, 1940).

In one of the study areas, where wild rodents and domestic rats comingled, plague was isolated from *R. norvegicus* during an epizootic in the wild rodents (Kartman *et al.*, 1958). One possible mechanism of plague transfer from the wild to the domestic rodents was indicated by studies with radioactively tagged *M. telchinum* which was found to migrate from *Microtus* to Norway rats under experimental conditions (Hartwell *et al.*, 1957). The public health significance of these ecological findings is seen in areas where suburbanization has creasted a period of "joint tenancy" between wild rodents, domestic rats, and humans. Although plague may not be demonstrable in some of these areas this does not necessarily imply its absence since in one study area it was found that plague remained quiescent for at least 18 months and then suddenly became resurgent without prior warning.

An attempt was made to understand these sudden surges in the plague infection rate by studying the relative susceptibility of the rodents. Small rodents found in the study area were trapped alive periodically for laboratory testing. Laboratory mice, rats, and guinea pigs were used as baseline controls to compare the susceptibility of the wild species of rodents. The intracutaneous route of inoculation was used in these tests because it simulates the flea bite; nevertheless, the volume inoculated (0.05 ml) was much larger than that injected by a flea. The results of these tests revealed a spectrum of response varying from very susceptible to highly resistant. The results confirmed the data obtained in a study in Santa Fe, New Mexico (Holdenried and Quan, 1956).

The rodents were classified into four main groups according to their relative susceptibility (Table 1). It was also found that some rodent species may be completely refractory to *P. pestis* inoculations; as the *Dipodomys ordii* in the Santa Fe study. However, no rodent species, of which sufficient individuals were tested, was found completely refractory in northern San Mateo County.

In all probability, the individuals of the host species which are highly susceptible are readily infected and die during a plague epizootic. Although the terminal sepsis of these dying rodents usually will serve to infect more fleas, the infected fleas left without hosts have but limited opportunities to transmit the infection. At the other extreme, individuals of host species completely refractory to plague do not develop terminal sepsis. However, these refractory animals may serve as vehicles in the spread of the infected fleas to other species. In species belonging to the middle two groups (Table 1) some of the infected individuals will die, while

Table 1.
Classification of rodent species according to plague susceptibility after intracutaneous inoculations of 0.05 ml of a *pasteurella Pestis* suspension.

Group	Succumbed to Approx. Number		Typical examples
	Virulent *P. pestis*	Mouse LD 50's	
Highly susceptible	1 to 10	< 1 to 1	*Mus musculus, Reithrodontomys megalotis*
Susceptible to slightly resistant	10 to 10,000	1 to 1,000	*Microtus californicus** *Peromyscus maniculatus***
Moderately resistant to resistant	10^4 to 10^7	10^3 to 10^6	*Rattus norvegicus*
Hightly resistant to refractory	> 10^7	> 10^6	*Microtus californicus* *Peromyscus maniculatus*

* From area D only (see Fig. 1).
** Santa Fe, New Mexico.

Table 2.
The seasonal susceptibility to experimental plague of three species of rodents from northern San Mateo County, California

Month, year of test	*Microtus californicus* (Highly Resistant)		*Microtus californicus* (Susceptible)		*Peromyscus maniculatus* (Highly Resistant)		*Rattus norvegicus* (Resistant)	
	A	B	A	B	A	B	A	B
Jan. 57	2/31	$> 10^6$	6/7	$< 10^4$	5/25	$> 10^6$	—	—
Feb. 55	8/44	$> 10^6$	—	—	2/17	$> 10^6$	7/16	10^5
Mar. 57	11/43	$> 10^6$	—	—	9/49	$> 10^6$	—	—
Apr. 55	5/24	$> 10^6$	—	—	1/9	$> 10^6$	—	—
May 54, 55	5/19	$> 10^6$	17/28	$< 10^4$	1/34	$> 10^6$	8/12	$< 10^4$
Jun. 55, 56	14/42	$> 10^6$	30/39	< 10	—	—	8/10	10^4
Jul. 56	3/19	10^6	4/4	$< 10^4$	1/10	$> 10^6$	2/5	$< 10^5$
Aug. 55	2/8	$> 10^6$	10/21	c. 20	7/32	$> 10^6$	—	—
Sept. 57	4/50	$> 10^6$	0/1	—	17/43	10^6	2/4	10^4
Oct. 54	5/42	$> 10^6$	—	—	4/46	$> 10^6$	12/24	10^4
Nov. 54	2/17	$> 10^6$	—	—	2/9	$> 10^6$	—	—
Dec. 56	23/68	$> 10^6$	4/5	$< 10^4$	2/42	$> 10^6$	—	—
Total, average	84/407	$> 10^6$	71/105	$< 10^4$	51/316	$> 10^6$	39/71	10^4

A - Number died/number used.
B - Approx. number *P. pestis* in LD50.

others will survive because the number of *P. pestis* transmitted by fleas may be less than the lethal dose. In such a pattern fleas would have opportunities to become infected on the dying rodent. The surviving rodents could not only carry and spread the infected fleas, but also might harbor plague bacilli either as an inapparent infection or as a prolonged one. It would appear that rodent species in the median resistant classes may have more important ecological roles in the maintenance of wild rodent plague than the other classes indicated here. Thus the extreme variability in the number of plague organisms transmitted by fleas is a possible mechanism for the perpetuance of rodent plague.

Another mechanism, which appears to be better substantiated, is the presence of heterogeneity in the susceptibility of a host species. Susceptible members of such a species would become diseased and infect fleas. The infected fleas would transmit the plague bacilli to the resistant members, which could serve as reservoirs. Although differences may be shown in the susceptibility to plague of *Microtus californicus* and *Peromyscus maniculatus*, both species were highly resistant to *P. pestis* inoculations. These species are found in large numbers in the plague foci in northern San Mateo County, California, and are considered to be reservoirs for sylvatic plague.

In the last four years approximately 1,200 live-trapped rodents, primarily 3 wild and 2 feral domestic species, were tested during various months of the year. The LD50's in terms of numbers of virulent *P. pestis* were evaluated or estimated, whenever possible, and are shown in Table 2. It can be seen that there were no significant differences in the LD50's of these species of rodents from season to season. Also, there were no differences in the LD50's of the more susceptible species of rodents or of the laboratory controls.

Preliminary analyses were also made with regard to the influence of age and sex of *Microtus* on susceptibility. These factors showed no significant effects.

An unusual finding was that the *Microtus* from a small peninsular area (Figure 1, area D), of approximately two to three square miles, were susceptible rather than resistant to *P. pestis* inoculations (Quan and Kartman, 1956). This area was approximately three miles from areas C or E, where *Microtus* were resistant and had been found to be naturally infected with

plague. Furthermore *P. pestis* has not yet been found in fleas taken from the D area. One plausible explanation for these differences may be found in the isolation of this small peninsula by a wide, heavily used cement concrete highway.

During six weeks of a recent epizootic in Area C, 61 rodent tissues and 2,202 fleas were cultured individually and then pooled for animal inoculation to test for presence of *P. pestis.* Of the rodents trapped, 293 *Microtus californicus* made up over 90 per cent, and 29 *Peromyscus maniculatus* made up 9 per cent of all hosts taken. Out of 61 rodents found in the traps either ill or dead, 16 were proved to have plague. The other rodents were released at their trap sites and periodically recaptured during the study. Out of the 2,202 fleas, 1,557 were *Malaraeus telchinum;* 247, *Hystrichopsylla linsdalei;* 198, *Catallagia wymanni;* and 146, *Atyphloceras multidentatus. M. telchinum* made up 70 per cent of the fleas, and the four species mentioned made up 98 per cent of all fleas collected.

The method used for the individual culture of the fleas to detect *P. pestis* was by triturating each flea with a glass rod in a small test tube containing 0.2 ml of broth, and then streaking a section of blood agar plate with the triturate which adhered to the rod. The agar plates were incubated at 28°C. After one day, triturates showing either *P. pestis*-like growth or gross contamination were segregated and inoculated into animals. About 15 to 20 per cent of the fleas had a heavy rate of contamination, showing 20 to innumerable colonies. Over 50 per cent had but a slight rate of contamination, yielding 5 or less colonies of microorganisms. No special precautions, therefore, were taken to avoid contamination other than keeping dirt from flea collections in the field.

The efficiency range of the culturing method was 68 to 87 per cent as compared with the usual animal inoculation method which gave a range of 59 to 98 per cent. The culturing method was uniformly sensitive at all levels of *P. pestis* in the fleas, while the animal inoculation method was less sensitive to fleas with small numbers of plague bacilli. Thus the average efficiency for the culture method was 76 per cent, while the animal inoculation method, skewed to the higher values, was 85 per cent.

When these two methods were used to detect *P. pestis*, the weekly infection rates in total fleas examined were 10.8, 5.6, 4.8, 4.3, 1.5, and 0.5 per cent, respectively, for six weeks. Although some individuals of each of the 4 flea species already mentioned (and also *Opisodasys keeni nesiotus*) were found naturally infected, the weekly rate of infection in *Malaraeus* was the only one which paralleled the rates above.

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AN INSECTICIDE-BAIT BOX METHOD FOR PLAGUE CONTROL IN CERTAIN AREAS OF THE PACIFIC REGION

LEO KARTMAN

San Francisco Field Station, San Francisco, California, U.S.A.†

Cases of human plague with high mortality rates have occurred in a number of Pacific areas in recent years (Kaul, 1949; Pollitzer, 1954). In Java, outbreaks have been traced to the Malayan house rat, *Rattus rattus diardi* and to *R. concolor; R. norvegicus* also was implicated. The flea *Xenopsylla cheopis* was the principal vector (Wilcocks, 1944). In Thailand, *R. rattus alexandrinus* was mainly involved, and *R. norvegicus* was a lesser factor. *X. cheopis* was the main vector (Park, 1941). In Viet Nam, Cambodia, and Cochin-China, *R. rattus rattus* and *X. cheopis* were the principal sources of the infection (Pollitzer, 1954). However, in 1943 domestic mice and *X. cheopis* were implicated in a limited outbreak at Saigon (Herivaux and Toumanoff, 1948).

In combating plague, it is now generally recognized that flea control should be carried out concomitantly with rodent control for the best result (Gordon and Knies, 1947; Kartman and Lonergan, 1955). In some cases flea control alone has been used with marked success (Macchiavello, 1946; McKenzie Pollock, 1948). Thus schemes for the simultaneous control of rodents and their fleas should be used as additions to a general program of plague control. It is fortunate that no significant resistance to DDT. or other insecticide has been noted in *X. cheopis* or in any other important flea vector of plague. DDT remains the insecticide of choice for plague and murine typhus control. Field tests have shown that a 5 per cent DDT dust is about as effective for the control of *X. cheopis* as a 10 per cent dust (Simmons, 1955).

Experience with an insecticide-bait box has shown that both domestic and wild rodents can be controlled with warfarin and that their fleas can be controlled with DDT powder picked up when the rodents visit the bait boxes (Kartman and Lonergan, 1955). More recent work with simplified bait boxes has shown that the fleas on various species of field mice are controlled both on the rodents and in their nests (unpublished). Direct evidence shows that rodents, which pick up DDT powder in the bait box, transport enough of it to their nests to kill the fleas there.

It is the purpose of this communication to recommend an insecticide-bait box for use in plague control in the Pacific region. Figures 1 and 2 are illustrations of a bait box which may be used in a combined operation of rodent and flea control. This is a simplified version of the bait box used in Hawaii (Kartman and Lonergan, 1955) and has been designed for greater ease of transport, low cost, and ease of maintenance.

These bait boxes can be placed at rodent holes and along rodent trails near buildings, in buildings, or in the field. In the field, they may be set from 35 to 50 feet apart when small rodents are involved, and from 50 to 75 foot intervals when larger species are the principal targets. Spacing of the boxes depends upon knowledge of the home range of the rodent. Placement of the boxes in and around buildings, on the other hand, depends primarily on locations near rat runs and holes. The usual method for control of fleas in buildings consists of dusting living quarters, outbuildings, attics, cellars, etc. with a 5 or 10 per cent DDT dust or a 5 per cent DDT spray where rats are known to be present. When indicated, DDT dusting of individuals, clothing, bedding, furniture, and domestic animals may be used. The bait box method in buildings can be used as a supplementary measure for ease of long term operation, and also in situations where the wholesale dissemination of DDT dust is contraindicated because of social or personal objections.

When used, the bait boxes are first placed in the area with unpoisoned food (rolled oats, etc.) for a one week pre-baiting period. Then a layer of 5 or 10 per cent DDT powder in pyrophyllite is spread uniformly on the floor board of each bait box (about 80-90 grams per box is sufficient). This is allowed to operate for about 4-6 days when the bait is changed to warfarin-treated rolled oats. The bait boxes are examined periodically to add DDT and bait when necessary. The length of the operation depends upon information gathered from periodic trapping of rodents to determine their prevalence and their flea indices. Examples of flea control data, obtained in field tests of the bait box method, are shown in Tables 1 and 2.

† From the Communicable Disease Center, Public Health Service, U.S. Department of Health, Education, and Welfare, Atlanta, Georgia.

Fig. 1.—End view of bait box showing bait container and DDT powder on floor; the bait box consists of a floor board 1/2 inch thick, 12 inches long, and 8 inches wide; it is covered by a U-shaped roof made by cutting a lard tin (9 1/2 inches in diameter and 12 1/2 inches deep) in half lengthwise; the roof may be fastened to the sides of the floor board or simply placed over the floor without fastening.

Fig. 2.—Side view of bait box showing DDT powder trails extending from both ends; note a vole, *Microtus californicus*, which has just left the box.

Table 1.

Effect of 5 percent DDT powder in bait boxes on the incidence of fleas on *Microtus californicus* in San Francisco.

Period	Treated Plot (DDT-Treated Bait Boxes Aug. 27 to Sept. 27)				Check Plot (150 Feet From DDT-Treated Plot)			
	Dates ('56-'57)	No. Animals/ No. Fleas	Mean Fleas	Percent Microtus Infested	Dates ('56-'57)	No. Animals/ No. Fleas	Mean Fleas	Percent Microtus Infested
Pre-treatment	8/15- 8/23	64/343	5.4	92.2	8/8 - 8/9	6/49	8.2	54.5
Treatment	9/5 - 9/26	162/2	0.01	1.2	9/11- 9/13	27/200	7.4	78.3
Post-treatment	10/2 -10/17	206/63	0.3	21.4	10/9 -10/17	32/176	5.5	99.9
" "	10/23-11/27	239/274	1.1	50.6	10/23-11/27	109/564	5.2	88.9
" "	1/8 - 2/7	56/59	1.0	41.1	1/8 - 2/7	40/126	3.2	82.5
" "	3/19- 5/2	63/58	0.9	42.8	3/19- 5/2	34/46	1.3	52.9

Table 2.
Effect of 5 percent DDT powder in bait boxes on flea incidence in nests of *Microtus Californicus* during the post-treatment period.

Treated Plot						Check Plot					
DDT-Treated Bait Boxes Aug. 27 to Sept. 27						(150 Feet From DDT-Treated Plot)					
Date ('56-'57)	Days After Treat.	No. Nests	Mean Fleas per Nest	Mean Fleas per Infest. Nest	Mean amt. DDT (mg.)	Date ('56-'57)	Days After Treat.	No. Nests	Mean Fleas per Nest	Mean Fleas per Infest. Nest	Mean amt. DDT (mg.)
10-5	8	7	0.1	1.0	2.1	10-17	20	7	9.0	12.6	0
12-19	83	4	0.2	1.0	1.1	12-19	83	3	14.6	22.0	0
2-6	132	3	0	0	1.0	2-6	132	4	11.5	12.0	0
4-10	195	4	33.5	33.5	0	4-10	195	4	38.5	77.0	0

In view of the fact that certain materials may not be available in some countries, it should be emphasized that modified versions of the bait box may be constructed from local materials. Thus in some areas large bamboo sections can be used for bait boxes. A small hole cut in the center of the bamboo (with plug when not in use) can be used to pour the bait into a small container secured at the center inside the bamboo tube. The DDT powder may be spread inside the bamboo section from both ends. Actually, many materials can be used to make the bait boxes. The principal consideration must be given to construction which protects the DDT from rain, and to bait box dimensions which accomodate both the smallest and largest rodents involved. As an adjunct to other operations, the insecticide-bait box method offers a cheap and efficient means of reducing the number of rodents and their fleas in rodent-borne disease control.

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DISCUSSION

H.J. COOLIDGE: How long does effects of DDT dusting last?

K.F. MEYER: About four weeks.

H.E. MCCLURE: Any flea resistance to DDT?

K.F. MEYER: No. Very rare in fleas.

OBSERVATIONS ON RODENT PLAGUE IN HAWAII

BERTRAM GROSS

Chief, Bureau of Rodent Control, Department of Health, Territory of Hawaii, Honolulu, Hawaii.

(Abstract)

1. The present status of plague infection in the known endemic plague region of the Hamakua District, Island of Hawaii, T.H., is reviewed.

2. A twenty-four year rodent retrieval record is presented. The data show that although the rodent species composition may vary from area to area, the native Hawaiian rat, *Rattus hawaiiensis* Stone, constituted 60.1 per cent of all rat retrievals and was the predominant rat species found in this plague region.

3. A tabulation of the extent of plague infection detected among the rodent species during the same period revealed that plague is found in all rodent species present and that 69.7 per cent of the infections detected were in *R. hawaiiensis.*

4. Figures on the seasonal incidence of rodent plague covering a forty-six year period showed that plague infection has been detected most often during the months September through March. It is pointed out that plague in rodents or their fleas has occurred every month of the year and that from a practical standpoint surveillance and suppressive measures must be undertaken through out the year.

5. Seven species of fleas are present. The three species most frequently found on rodents are *Xenopsylla cheopis*, *Xenopsylla vexabilis hawaiiensis* and *Leptopsylla segnis.* All five of the rodent species present are infested by these three species of fleas.

6. The rodent flea patterns varied greatly from area to area. There were certain areas far removed from buildings where *X. cheopis* were found and *X. vexabilis hawaiiensis* were not. The reverse was true in other areas. This indicates that small geographical differences within this plague region may influence the flea patterns.

7. A study of the distribution of fleas among rodents cage trapped in three separate field areas showed that *R. norvegicus* is consistently more highly parasitized with *X. cheopis* and *X. vexabilis hawaiiensis* than are the other rodent species.

8. Data presented do not support the contention of other workers that the outdoor *X. cheopis* index in the Hamakua plague region is low and inadequate for the spread of plague and, therefore, the role of *X. cheopis* in the perpetuation of plague in the fields assumes greater importance.

9. The desirability and possibility of evolving a low cost method of applying insecticides to rodent burrows and nests in the field is discussed.

10. Plague suppressive measures are evaluated including the application of insecticides and the importance of good sanitation and inhousing.

DISCUSSION

W.W. CANTELO: Type of baits and bait stations?

B. GROSS: Trap lines are 50 feet apart with poison stations at midpoint. Two types of poison utilized: (a) bread and phosphorus, and (b) zinc phosphide with rolled oats, wheat, or barley at conc. of $\frac{1}{2}$ lb. zinc phosphide per 100 lb. grain with addition of lime. Zinc torpedoes are broadcast by hand in caves and gulches.

PLAGUE IN THAILAND

MALI THAINEUA

Provincial Health Officer, Ubon, Thailand.

(Abstract)

Plague has been endemic in Thailand for many years. The first case was reported in Bangkok in 1904. The infection was believed to have been imported from India. No definite records were available before 1913. There were two waves of plague epidemic from 1913 to 1934 and from 1938 to 1952 respectively. A severe epidemic occurred in Korat in 1917 and more than 500 deaths were reported. Surprisingly there was not even a single case of plague reported from the southern part of Thailand. This may be due to incorrectness of reporting.

From 1938 plague cases have been reported every year. In 1952 it was decided that greater effort should be made to control the disease. Therefore with the aid of ICA in 1952 three permanent laboratories for detection and control of rat-born diseases were established in three plague endemic areas in Thailand. The following methods of control were carried out:- DDT dusting and spraying for keeping down the *X. cheopis* population, rat poisoning-trapping, and improving sanitation by eliminating rat harbourage. These three laboratories with good co-operation from the local authorities were very successful in this campaign and no single human case of plague has been reported since 1953.

DISCUSSION

J.L. HARRISON: Where does *Rattus rattus thai* occur most?

M. THAINEUA: Open rice fields and houses.

A.G. SEARLE: Does *Rattus r. tikos* occur here?

J.L. HARRISON: May be same as *R.r. thai.* Do Bandicoots enter houses here?

M. THAINEUA: Very rarely.

J.L. HARRISON: Suspects bandicoots involved in plague in Rangoon.

A.G. SEARLE: Is housemouse white bellied or grey or brown bellied?

J.L. HARRISON: Same as Malayan ones, grey. Are we equating *R. hawaiiensis* with *R. exulans*?

B. GROSS: Yes. Comments then given on appearance and life habits of this rat.

Symposium: ***Contributed Papers in Zoology***

JAPANESE EXPEDITIONARY ACTIVITIES IN BIOLOGICAL SCIENCES IN POSTWAR ASIA

TADAO UMESAO

Laboratory of Ecology, Institute of Polytechnics, Osaka City University, Osaka, Japan.

This paper intends to introduce to the attendants of the present Congress ‘he activities and results of the recent Japanese expeditions in Asia, which are as yet little known in other countries, with special references to biological sciences, including botany, zoology, and anthropology.

Before the War, the Japanese people had their main interests in the Continent, the countries of the northeastern part of Asia, Korea, Manchuria, Mongolia and China. In these areas, Japanese scientists had carried out the active works in the fields of the basic sciences as well as the applied sciences.

After 1944, however, it has become almost impossible for the Japanese scientists to continue their works in these areas. They have turned their eyes to the southern part of Asia.

Geographically speaking, the countries of South-East Asia are very near from Japan. But, after the War, there have been some difficulties for Japanese to perform scientific field works in these areas. To the regions of South East Asia, I will mention later. The earliest post-war expeditions from Japan concentrated to the mountainous area of northern India.

In the following review, two regions are especially mentioned. The one is Central Nepal and the other is the Karakoram-Hindu Kush Range extending from West Pakistan to Afghanistan.

NEPAL HIMALAYA

In 1951, some scientists of Kyoto University organized the Fauna and Flora Research Society (FFRS) to investigate the little known parts of Asia and above all the Himalayas in cooperation with the Academic Alpine Club of Kyoto (AACK). Now, the society includes twenty one professors of three universities in Kyoto and Osaka. After the establishment, the society began at once to organize a scientific expedition to Central Nepal Himalaya under the presidentship of Dr. Isawo Namikawa, Prof. Emeritus of Kyoto University. The plan was later accepted by the Japanese Alpine Club (JAC) and in 1952 a reconaissance party was sent by JAC to Nepal in order to find out a possible route to the summit of Manaslu (8125 m), one of the least known peaks of so-called Himalayan Giants at that time. On the trip round Manaslu Massif, the reconaissance party successfully found a promising climbing route on the eastern slope of the peak. From 1953, on the climbing party of JAC began the assault on Manaslu, and after several frustrated trials, the Japanese party finally reached the summit in May 1956.

The 1952 reconaissance party was headed by Dr. Kinji Imanishi, an FFRS member known as eminent ecologist and alpinist in Japan. Anothor member of the soiety, Prof. S. Nakao joined the party as botanist. They brought back a considerable amount of biological collections. To the first climbing party of 1953, FFRS again sent two members, Prof. Nakao and Prof. J. Kawakita, a geographer. They skirted around the three great massifs of Nepal Himalaya, the Annapuraña, the Manaslu-Himal Chuli and the Ganesh Himal. Botanical collections of the preceding year was greatly enriched by Nakao, and Kawakita made an extensive observation on the anthropology of the region. An anthropological collection was brought back for the Ethnological Museum of Tokyo.

In the postmonsoon season of the same year, a small party of AACK attacked Annapurana IV (7525 m), but was driven back by strong wind at 7200 m. Two members of the party were the students majoring in horticulture. They also brought to Kyoto University specimens and seeds of wild and cultivated plants as well as some insects.

The materials collected by these expeditions were entrusted to FFRS and thoroughly investigated by the members of the society and many other specialists in Japan. The results have been published by the society in three volumes, "The Scientific Results of the Japanese Expedi-

tion to Nepal Himalaya 1952-53" edited by Dr. Hitoshi Kihara, Director of the National Institute of Genetics. They are written in English and include some 1400 pages.

The first volume is "Fauna and Flora of Nepal Himalaya (1955)." Most of the volume is dedicated to the taxonomy of plants and insects collected during the expeditions. Collection of plants not only phanerogamous but also ferns, mosses, fresh water algae and lichens, was most complete. For general information, the number of collected plant species is enumerated in table 1.

Considering the restricted area and season of the collections, this result, especially the high percentage of new and newly recorded species, should be evaluated. The number of phanerogamous species listed in Landon's *Nepal* (1928) was 1672.

According to Prof. Kitamura, who compiled vascular plants in the volume, the alpine flora of Himalaya is closely related to those of Eastern Tibet, Western China and partly Formosa. It is also very interesting that some plants collected by Rev. Ekai Kawaguchi, a Japanese Buddhist who visited Tibet through Central Nepal in 1899-1900, were rediscovered by the present expeditions and one of them was new to science.

The zoological collections from Nepal are not numerous and restricted to insects owing to various difficulties in collecting. Butterflies, dragonflies, fruitflies, mayfly nymphs and rice weevils were described by 5 experts. The number of butterfly species collected amounted to 100 and many of them were new to Nepal.

Prof. Nakao presented a brief note on the natural vegetation of central Nepal Himalaya. And, at the top of the second volume "Land and crops of Nepal Himalaya (1956)", Prof. Kawakita described the major types of vegetation in detail as related to climatic and edaphic conditions. He recognized 6 altitudinal zones of vegetation from the subtropical forest (evergreen seasonal forest) of sal tree to the alpine zone. To the west of the Manaslu Massif, the climate tends to be arid and dense forests of subalpine and temperate conifers gradually give way to open woodland of pine and juniper, and finally to the desert-like vegetation composed of dwarf brushes armed with thorn or spikelets.

Native agriculture of Nepal was studied by Kawakita and Nakao. The former thoroughly analysed the crops zones along altitudinal gradient and discussed the influence of climatic and cultural factors upon the cropping system. He also made some suggestions on the agricultural improvement.

Cultivated plants in Nepal were studied. They are mostly collected as seeds and grown for observation in Japan. Some 30 specialists, including one from U.S.A., present the result of morphological, taxonomical, cytological and agroecological studies on rice, maize, wheat, barley, oat, African millet, and some other cereal crops, grain Amaranthus, buckwheat, hemp, morning-glory, legumes, several kinds of vegetables, etc. Several materials of native plant drugs were also studied.

According to Dr. Namikawa's generalized statement, not any characteristics of the Nepalese crop varieties seem useful for the improvement of Japanese varieties. Nepalese varieties of legumes, cucumbers and other crops are either very late to flower or easily susceptible to pests under

Table 1.
Plants collected by the Japanese Himalayan Expeditions 1952-53.

Investigator	Materials	Species	New species	New variety and form	Remark
S. Kitamura	Ferns	34	0	0	
	Gymnospermae	14	0	0	
	Angiospermae				Ca. 300
	Monocotyledoneae	110	3	0	species
	Dicotyledoneae	812	34	15	are new
	Characeae	2	—	—	to Nepal
Y. Horikawa	Mosses	62	—	—	
M. Hirano	Freshwater algae	184	1	4	
Y. Asahina	Lichens	62	2	1	
	Total	1,280	40	20	

Japanese climate. They are more or less primitive in their characters as compared with Japanese crops.

The third volume of the Scientific Results of the Expeditions includes above all the comprehensive account of Prof. Kawakita's ethnogeographical study on the natives. He describes the distribution of ethnic and cultural elements along his route, agriculture, animal husbandry, transportation and commerce, settlement, territorial organization, tribes and castes and so forth. Special attention is paid to the religions of both Hinduistic lowland and Lamaistic highland and he points out the possible existence of a primitive shamanistic religion among mountain inhabitants which still survives as relict under the recent predominance of the two powerful religions. He made the intensive survey of a Tibetan village, Tsumje, situated at the altitude of ca. 3500 m on the uppermost reaches of Buri Gandaki (River). He stayed there for 40 days studying all phases of its life. A tentative conclusion on the structure of Tibetan life contains many interesting and original points of view, but it may take too much space and time to introduce only the outlines.

Mr. Y. Huzioka also contributes to the volume on the results of Rohrschach test obtained from the inhabitants of Tsumje, a Tibetan village. The personality make-up of the village, he concludes, is isolative, more self-gratifying than social. Other aspects of the study will be presented by the author himself at the present Congress.

KARAKORAM-HINDU KUSH RANGE

Let us now turn to the second area, Karakoram-Hindu Kush. In 1955, Kyoto University sent the Kyoto University Scientific Expeditions to Karakoram and Hindu Kush (KUSE 1955) under the general leadership of Prof. Kihara. 12 sceintists including a surgeon, most of which were the members of FFRS, 2 cameramen, a reporter, a liaison officer from Pakistan and two interpreters from Pakistan and Afghanistan constituted the expedition. During the period from April to October, the expedition covered in several parties the extensive area through India, Pakistan, Afghanistan, Iran and finally to the southern coast of the Caspian Sea.

The Karakoram party headed by Dr. K. Imanishi travelled through high peaks of central Karakoram along the three magnificent glaciers, Hispar, Biafo and Baltoro, and carried out geological, botanical and anthropological investigations. Two geologists also traversed the upper reaches of the Indus River from Gilgit to Askole. Geological studies are now continued in adjacent area as stated later.

Other members of the expedition entered Afghanistan from the Baluchistan border in early June. One of the main object of the botanical party was to collect materials in order to verify the hypothesis of Dr. Kihara on the origin of cultivated wheat. From his long years' genetical and cytological study, he reached the conclusion that the cultivated wheat *(Triticum vulgare)* must have originated from the hybridization between Emmer wheat and *Aegilops squarrosa*, a close relative of the genus *Triticum*. Actually he succeeded by crossing these two species in the artificial synthesis of new hexaploid wheat, which closely resembled *Triticum vulgare* in their morphology. He considers that the cultivated wheat had most probably appeared at least 4000 years ago in Transcaucasus, where the ranges of distribution of wild Emmer and *Aegilops squarrosa* overlap each other. Throughout their long travel from Quetta of Pakistan along ancient Silk Road to the Caspian Sea, Dr. Kihara and Prof. K. Yamashita found *Aegilops squarrosa* growing everywhere as weed in wheat fields, and in some restricted localities growing together with cultivated Emmer wheat. Many specimens of *squarrosa* and other species of *Aegilops* were brought to Japan and are now under investigation. But their experiences seem to support Kihara's hypothesis that Transcaucasus must have been the native place of cultivated wheat.

Another member of the botanical party was Prof. Kitamura of Kyoto University. He made several collecting trips from Kabul in the eastern half of Afghanistan. Experiences in Nuristan or the southern slope of central Hindu Kush were especially fruitful, where he found the westernmost extention of the Sino-Japanese Flora. Abundant collections of wild and cultivated plants from Karakoram-Hindu Kush Range are now being studied by several Japanese experts.

The anthropological party of the expedition was composed of four Japanese members. As a human ecologist I joined the party. The main aim of the party was the discovery and research of Mongolian tribe in Afghanistan. It has long been known since 1906 that there lives somewhere in Afghanistan a Mongolian tribe, Moghol as the tribe is called in Afghanistan, speaking apparently Mongolian language, but no one has yet succeeded in visiting its native land.

The expedition succeeded in discovering the village of Moghols in the midst of Ghorat District, a mountainous region of West Afghanistan. Linguistic and ethnographical research was carried out. Plant and insect specimens brought back to Japan may be the first collection from the district.

The collections and materials brought by KUSE are now studied in Japan supported by financial aids from the Ministry of Education. The scientific results will be published from next year onwards by FFRS.

In 1956 and 1957, the Exploration Club of Kyoto University sent two small expeditions to Eastern Hindu Kush in cooperation with Punjab University, Lahore, Pakistan. Japanese members of the 1956 party consisted of two students in biology and Assist. Prof. K. Huzita of Osaka City University who was a geological member of the Karakoram Party of 1955. They covered the area west of the Hunza River. In this year, Prof. S. Matushita, who collaborated with four Japanese students in geology and forestry, visited Swat Province, a little known tribal territory on the northwest border of Pakistan. Several geologists and botanists of Punjab University also joined the party.

In ending this brief review, I wish to tell you that our interest is now turning to S.E.-Asia especially to the regions covered by primaeval forests. Post-war activities of Japanese scientists in these areas are almost nil.

In the early months of this year, two agronomists from Hyogo Agricultural College visited Laos, Cambodia and Viet-nam, with special interest in rice cultivation in these areas.

On the problem of rice cultivation, a new attempt is being made. The Ethnological Society of Japan organized an expedition which intends to collect ethnographical data of rice cultivating peoples of these areas. They are now working in Laos and Cambodia. Although most members of the expedition are of the cultural sciences, such as linguists, ethnographers, and historians, two of them are specialists of morphology and genetics of rice. The Society will continue the work in the following years.

The latest one is the Osaka City University Biological Expedition to South East Asia. I and my five colleagues are staying in Bangkok. All members are ecologists. Two of them are plant, two are animal and the other two are human ecologists. At least three members of Chulalongkorn University will join us. After the Congress is over, we are going to start towards northern part of Thailand, and later, visit Laos, Cambodia and Viet-Nam.

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Japanese expeditions covering biological fields in post-war Asia.

Year	Region	Leader	Organization
1952	Central Nepal	K. Imanishi	JAC
1953	Central Nepal & Manaslu	Y. Mita	JAC
1953	Annapurna IV	T. Imanishi	AACK
1954	Manaslu & Ganesh Himal	Y. Hotta	JAC
1955	Karakoram & Hindu Kush	H. Kihara	Kyoto Univ.
1956	Manaslu (ascent)	Y. Maki	JAC
1956	Eastern Hindu Kush	K. Huzita H. Begg	Kyoto Univ. & Panjab Univ.
1957	Swat Himalaya	S. Matsushita	Kyoto Univ.
1957	Cambodia & Laos	S. Sato	Hyogo Agricultural College
1957	South East Asia	N. Matsumoto	Ethnological Society of Japan.
1957	South East Asia	T. Umesao	Osaka City Univ. & Chulalongkorn Univ.

DISCUSSION

N.A MEINKOTH: Any zoological work done on the expeditions to Nepal and Afghanistan?

T. UMESAO: Yes, results will be published later.

E.H. TAYLOR: Were all groups of animals sampled?

T. UMESAO: No, only certain groups.

A.G. SEARLE: What kind of animal ecologists are going on your next trip?

T. UMESAO: A primatologist and an entomologist.

E.H. TAYLOR: Where next after your trip through Thailand?

T. UMESAO: Not yet determined. Finances for further trips not yet available.

FIELD STUDIES ON THE SOCIAL LIFE OF PRIMATES IN JAPAN

SYUNZO KAWAMURA

Osaka City University, Osaka, Japan.

A group of Japanese ecologists set out in 1948 a systematic study of the comparative social ecology on higher animals. It began with two field studies, observations of the semi-wild native horses at Point Toi in Kyushyu by Dr. K. Imanisi, and of the famous herd of sanctuary deer in Nara Park in central Japan by me. We took up a characteristic intensive method in these surveys, which was a successive observation, long enough to make clear the changing phases of the animal community, based on accurate recognition and discrimination of all the individuals of the group.

In 1950, Dr. Imanisi, Mr. J. Itani and I went to Kyushyu for the first investigation of natural communities of the Japanese macaque, Macaca fuscata fuscata, and since that time we have called ourselves Primates Research Group. Prof. D. Miyazi (Kyoto Univ.) became the chairman of the group, and Dr. K. Imanisi, Mr. N. Hazama, Mr. M. Kawai, Mr. K. Tokuda, Mr. H. Mizuhara, Mr. M. Yamada, Mr. Y. Huruya, Mr. S. Maegawa and I its members. This group is a branch of the Kyoto School of animal ecology.

The horses, the deer, the domesticated rabbits and the mice were actually in our objects, but our primary interest was in Primates, because of their phylogenical kinship to human beings.

The observation of rhesus macaque and crab-eating macaque was done in zoo, as well as of Japanese macaque in laboratory cage, but most of all we have done field studies of the wild groups of the native macaque.

In the course of adopting our intensive method with monkeys, we were obliged to go through the following three stages: first we pushed through forest and bushes of arduous mountains, following after the cautious, cunning and nimble animals. General life history with vocal communications and some other behavior of the monkeys was thus investigated. At the second stage, we succeeded to approach the monkeys in close distance, after patient endeavour to provide them with food. Thus we elaborated the individual discrimination by recognizing the face of each animal, and on this basis, we analyzed many points of the social functions and forms of the community. At the third stage, we stepped into a long term observation to see the development of individuals as well as of groups.

Now we have 16 natural groups, 2 migrated natural groups and 2 artificially composed groups which are ready for any observation. More than half of them have been thoroughly investigated, and so we are now able to compare group after group on many points of social phenomenon.

i) Mt. Takago (Tiba Pref.); 1 group of 7 groups became tamed.
ii) Okinosima Islet (Aiti Pref.); the Syodo-T Group was artificially imigrated into this small islet. (We prepared the Syodo-O Group for imigration.)
iii) Japan Monkey Center (Aiti Pref.); founded in 1956. The first journal of primatology, "Primates" is published by Japan Monkey Center (J.M.C.).
iv) Arasiyma (Kyoto Pref.); there is 1 tamed group.
v) The Minoo valley (Osaka Pref.); there are 2 tamed groups.
vi) Tomogasima Isl. (Wakayama Pref.); 1 artificially composed group.
vii) Tubaki (Wakayama Pref.); 1 tamed group.
viii) Syodo Is. (Kagawa Pref.); 2 tamed groups and 1 wild. Another 2 groups were captured for imigration.
ix) Mt. Gagyu (Okayama Pref.); 1 tamed group.
x) The Taisyaka Valley (Hirosima Pref.); 1 tamed and 2 wild.
xi) Sirahama (Ehime Pref.); 1 tamed group.
xii) Mt. Takasaki (Oita Pref.); 1 tamed group.
xiii) Kosima Isl. (Miyazaki Pref.); 1 tamed group.
xiv) Point Toi (Miyazaki Pref.); 1 tamed group.
xv) Yaku Is. (Kagosima Pref.); numerous monkeys (M.f. Yakui) live in a wild state. They are the important sources of experimental monkeys in Japan.

There are another 3 tamed groups in Japan, which has not yet been surveyed.

The Japanese macaque is endemic to Japan, and is distributed over mountainous places in Honshyu, Sikoku and Kyushyu. We estimate the whole population at 50,000-100,000 heads. They live in groups of as many as 30-150 heads in moderate size, but the group population varies from scores to several hundreds.

They feed on many sorts of vegetable, such as fruits, nuts, seeds, root stocks, flowers, buds, shoots, leaves, twigs, barks, saps etc. It is remarkable that these forest dwellers eat so much grass. They are also insect eaters, and some of them take land snails. In coastal regions, they are known to eat shell-fishes on beach rock. They never take meat of any kind, but bird eggs are favorite food among some monkey groups. There are differences of food habit between groups. Babies may learn the foods of their group, mainly from their mothers.

Each group leads its own nomadic life within the home range, the extent of which varies from within 1 square kilometre to more than 10 square kilometres. There is no direct correspondence between the extent of the range and the population size. Historical and social factors should be seriously considered.

The pattern of nomadic life is specific to each group. Considerable number of groups have their centers of nomadism, and from there begin circuital movements which repeat fairly often. Duration of each nomadic cycle vary from 1 day to about 2 weeks. But some groups migrate 4-8 kilometres seasonally and perform the long cycle of nomadism. Another type of cycle occurs in some groups which have slow movement day after day within their rather vast home range. The Takago-A Group belongs to the last type, and the Takasaki Group belongs to the first type which has a "Base" of nomadism and all short cycle of nomadism.

Although the secondary sex ratio in the group generally indicates the rate 1 : 1 or so, we have found the socionomic sex ratio varied considerably between groups. In the Minoo B group, there are 9 fertile females against 1 adult male, while three groups in Syodo Is. (the Syodo-O.S.T. Group) the number of matured male is just the same or exceed a little that of mature female. The population piramids of the groups are generally steady.

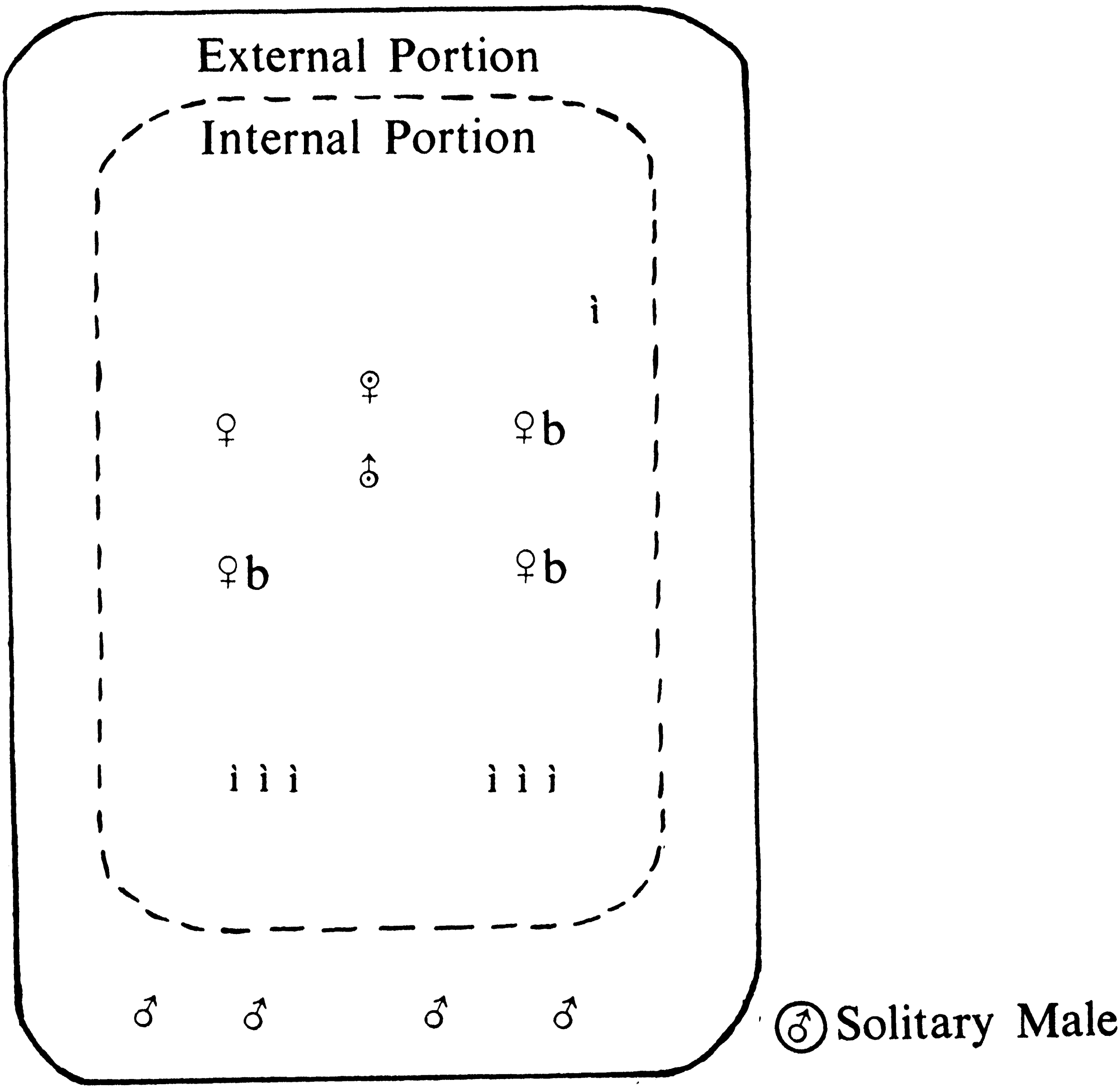
The generalized view of the group organization is as follows. The natural community of Japanese macaque consists of 2 segments. One of which is the internal portion of the group including leader males, young and adult females, infants and babies. The ordinary males of our term form another segment which is the external portion of the group. (Fig. 1) Such as resting, feeding or slow moving times, these two segments usually lay concentrically. But when rapid movement occurs and the group march in a single line, the ordinary males go at the top and the rear, placing the internal portion between them.

The problem of spacial distribution of individuals in the group has been investigated and confirmed in detail. One of the investigation was my distribution test on the Kosima Group in 1954. Here I must refer to the solitary males and collective male parties, both of which are the male monkeys that have left the maternal group. Solitary males are commonly seen in all the localities of monkey habitat, while the male parties are rarely recorded. The male parties are semi-permanent, because they accept new partners that come from adjacent groups. Solitary males often venture off to considerably large area, and some of them wander away for ever. When the sexual season begins, most of solitary males and male parties appear again in the vicinity of the group, and some of them apparently are born of another group. Solitary males occasionally return to their original group, and even rise to the status of the leader male.

I have mentioned above that the common style of the Japanese macaque community, where the leader males and the ordinary males are seen. In smaller groups, the population of which is less 30 heads, we have usually found 1 leader male, but in larger group the number of the leader males is counted 2 or more. The largest number of leaders of a group was 6 heads, which was recorded on the Takasaki Group and on the Syodo-K Group. Although the population of the Takasaki Group has increased from 220 (1952) to 520 (1957) within these 5 years, the number of leader males has decreased from 6 to 4 during the same period. Many facts are available to indicate that there is no direct correspondence between the population of the group and the number of the leader males, but it may be generally concluded that the Japanese monkey reach the high equilibrium of having 1 leader male per every 20-30 heads.

The role or function of a typical leader is as follows. Usually, the ordinary males are the guards of the group, but once a situation became serious, the leader male appears in front of the enemy, or manages the escape of the whole group.

Total 20 Individuals



♂ Leader Male ♀ Chief Female i Infant

♂ Adult Male ♀ Adult Female b Baby

♂ Adoles. Male

Fig. 1.—The Kosima Group at Nov. 1952.

He occasionally climbs up to the top of a tall tree, and surveys the conditions or circumstances of his groups, then he shakes the tree vigorously with loud uttering. This tree shaking behavior accompanied by uttering is also performed when he gives the starting signal to his monkeys, when passing over ridges or when enemy menaces.

Another remarkable function of the male leader is the "controlling." He stops any quarrel happening in the group, by attacking or menacing the individual causing the quarrel.

The leader males and the ordinary males are easily distinguished from one another by their location and by their function in the group, although there are exceptions, when the difference is obscured by marginal individuals.

In larger groups, scattered over the internal portion, the leader males have a good team work under a linear dominance rank system. Each leader male has his own role about this poliarchal team work, but some of them have no important job in their team.

In the case of the Syodo-K Group, the division of labour among the leader males was as follows.

The first male : he is old and retired from serious job.

The second male : he did actual leading service. He was the axis of the group, but a respected first male as well.

The third male: he is next to the second male in leading service.

The fourth and the fifth male: they were the complemental leaders.

The sixth: he has the special job in giving alarm and piloting.

There are seldom fights or duel for dominancy in the natural group of Japanese monkey, and so old leaders decline slowly to the declining leader status. It seems that there is no sudden change, through this process. In the Syodo-S group, the oldest male that is estimated about 30 years old still holds the predominant position of leader. Although he can no longer climb trees well.

The ordinary males are the young or adult males who had been rejected from entering the internal portion by leaders and females. But males go out to the external portion rather naturally when they are 3-4 years old.

In some groups there are marginal individuals between the leader and the ordinary male. They are the adult and the adolescent center male of our term, and they are tolerated by leaders to live in the internal portion. There is a remarkable difference between the group that has the center male and the group that has not, on the design of group construction. In other words, there is a variety on group integration. Some of the center males were sons of higher rank females.

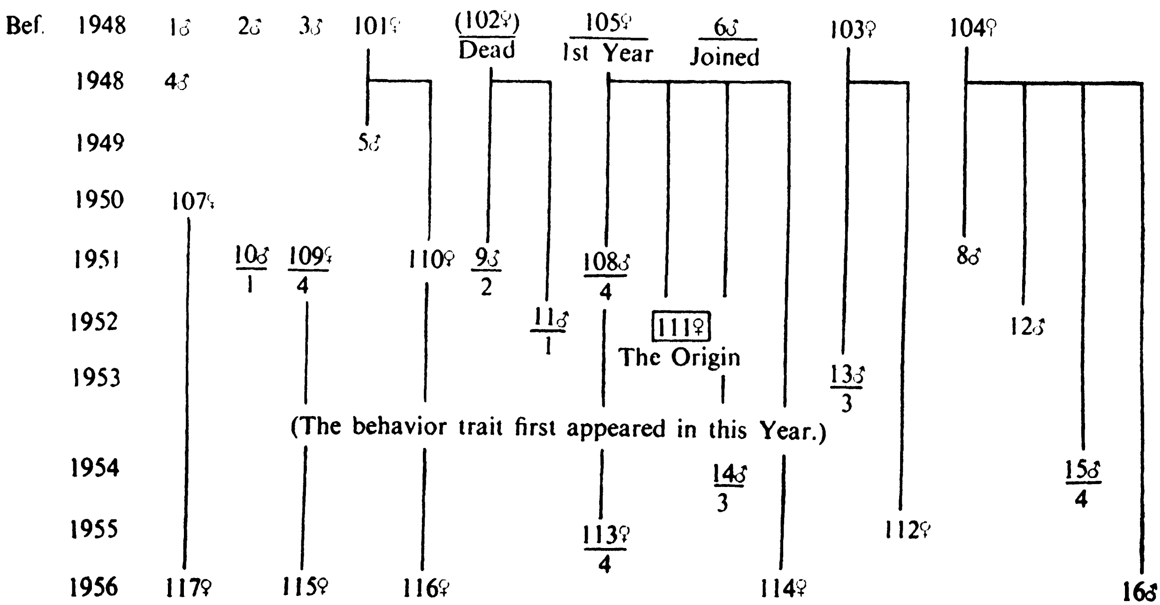


Fig. 2.—The "Potato-Washing-Behavior" originated from an infant female in 1953, and spreaded slowly but steadily over a half of the Kosima Group in three years. I trace here its process on the lineage of the group.

There are a few females who have a special contact with the predominant leader male. By this she wins the highest position among females in dominancy, we call her the chief female. The typical chief female was found in the Kosima Group and in the Minoo-A, B Group. Social relation between the predominant leader and the chief female continues all year round, including non sexual seasons. The chief female does a part of the role of the leader male, for instance, the tree shaking and the controlling.

The population, the socionomic sex ratio and members of each status of five groups are shown on Table 1. The declining leader is not seen in these 5 groups, but he was in the Taisyaku-A Groups. Next there is the intergroup relationships among groups.

In Syodo Is. there were 5 groups in the central hill. They seemed to segregate their habitation pretty well, although there were some overlapping portion between them.

I think they settled their borders according to the physiognomy of mountains, and their own preference. For instance, no one of the Syodo-O group ever went westward beyond a shallow stream of the upper Tatibana River, whereas they used to proceed over more difficult valleys.

In Takago district, a more complicated relationship was found. Some of borders are more sociologically settled than Syodo Is. They seem to avoid meeting each other but, lesser groups avoid other groups more often than the larger ones.

The next problem is that how a new habit or custom is introduced into the group. On this problem the Japanese monkeys afford some interesting data of sub-human culture.

We observed a process of a social learning in the Minoo-B group. All the members of the group learned of wheat as a food from a young-adult male, Nasio, who recently returned from a male party which had the habit of wheat eating. They completed this learning in 4 hours.

Fig. 2 shows the "Potato-Washing-Behavior" that originated from an infant female in 1953, and spread slowly but steadily over half of the Kosima Group in three years. The process on the lineage of the group, can be traced.

Each group of Japanese macaque has so many specific behavioral types in selecting its food, in leading its nomadism, in organizing its community, etc. Vocalization and some other sign behaviors are also specific to some groups. It is believed that part of them were acquired or learned by the monkeys and later became traditions of the group and then these are their culture.

Table 1.

Population, Socionomic Sex Ratio and Members of Each Status of 5 Representative Groups.

		1952	1956	1957	1955	1957	1957	1953	1957
Population		20	28	62	67	98	150-160	ab.260	ab.520
Socionomic Sex Ratio ($\frac{f.}{m}$)		1.25	1.13	1.42	2.60	2.33	5.00-5.20	2.50	1.69
Leader Male		1	1	2	2	3	6	6	4
Center M.	Adult	—	—	1	—	—	1	—	—
	Adolescent	—	—	1	2	1	—	—	—
Declined Leader M.		—	—	—	—	—	—	—	—
Ordinary M.	Adult	2	3	3	3	3	3	30	85
	Adolescent	1	4	5	3	9	—		
Elder Infant M.		1	4	4	10	10	20-25	30	40
Chief Female		1	1	—	1	1	—	—	—
Ordinary F.	Adult	4	4	13	13	24	35-37	60	130
	Adolescent	—	4	4	12	10	15	30	20
Elder Infant F.		1	—	2	5	8	13-15	30	40
Younger Intant (M. & F.)		6	2	17	10	14	26	30	120
Baby (M. & F.)		3	5	10	6	15	31	45	86
Semi Solitary Male		—	2	2	—	2	2	2	ab.10
Solitary M.		1	—	—	1	1	—	2	
Collective M.		—	—	—	10	5	14	—	—

DISCUSSION

N.A. MEINKOTH: Do the monkeys pay attention to the observer?

S. KAWAMURA: Yes, but these can be distinguished.

H.J. COOLIDGE: Commends the work done at the "Private Institute" in Japan. This is rather unique, and will contribute to our understanding of comparative behavior.

Dr. Coolidge then commented on the nature of the Institute and primate studies in progress in Japan.

CYCLIC CHANGES OF MOUSE EPIDERMAL CELLULAR POPULATION IN CORRELATION WITH THE HAIR FOLLICULAR ACTIVITY

HSU-MU LIANG

Biomorphic Department, National Defence Medical Center, and Zoological Institute, Academia Sinica, Taipei, Taiwan, Republic of China.

INTRODUCTION

Pinkus (1927) held the concept that replacement of the desquamating and keratinized cells in the epidermis was by mitotic division of the basal cells. Storey and Leblond (1951) found that this process was at such a rate that the neoformation of cells balanced exactly the cell loss due to desquamation. Therefore the assumption is that the number of cells in epidermis remains constant. In other words, the epidermis is a "steady system" in regards to its cellular content.

On the contrary, one of the epidermal appendages, the hair follicles, undergo a wave-like pattern of degenerating and regenerating phases of growth. This cyclic phenomenon is well known to exist in laboratory animals by many investigators (Dry, 1926; Butcher, '34, '51; David, '34; Schwanitz, '38; Lubnow, '39; Kaliss, '42; Taylor, '49; Walbach, '51; Chase *et al.*, '51; Andreasen, '53; and Liang and Cowdry, '54). In association with different phases of hair follicular cycles, changes of epidermal thickness were reported (Andreasen, '53; Chase *et al.*, '53; and Liang *et al.*, '54).

However, the total cell counts and the numerical proportions of different kinds of cells in the normal epidermis in correlation with different phases of the hair follicular activities are still wanting. This information is important for the thorough understanding of skin under normal and experimental conditions.

The established fact that plucking of club hairs will initiate growth of the succeeding hair generation (Collins, '18; David, '34; Schwanitz, '38; and Chase, '46, '49a, b) makes it possible to control hair follicular cycles which can be divided into growing (Anagen), degenerating (Catagen) and resting (Telogen) stages (Dry, '26; and Chase *et al.*, '51).

MATERIAL AND METHODS

In the present experiment 50 normal female mice of C57 black strain were used. Pieces of skin from the dorsum of known phases of hair follicular growth were excised. Half of the skin from each animal was fixed, embedded in paraffin, cut in serial sections both cross-wise and longitudinally, and stained with hematoxylin and eosin. The other half was treated with cold acetic acid (Liang, '47), separated into epidermis and dermis, stained with hematoxylin, and prepared into whole mounts. The thickness of each epidermis was measured with an eye-piece micrometer under oil immersion objective. The total epidermal nuclear counts per $\overline{mm}^2$ and the population of different kinds of cells were estimated according to Abercrombie's formula (Abercrombie, '46).

RESULTS AND CONCLUSIONS

It was found that the epidermis was thickest (31.06μ) during early anagen phase. The thickness increased abruptly from telogen to early anagen, and then dropped in late anagen phase during which it was the thinest (11.48μ). From then on the thickness of epidermis remained with little change passing through the telogen stage (12.28 μ).

Pari passu with changes of epidermal thickness, the number of the total epidermal nuclear counts per $\overline{mm}^2$ changed accordingly. It was greatest (21,600) during early anagen and then dropped gradually in late anagen when the nuclear count was the least (13,700). From now on it increased through catagen (14,100) to telogen (15,000) which then shot abruptly again to its peak at early anagen.

The numerical proportions of different cells also fluctuated. The most obvious change occurred in the granular and spinous layers in which the cells in the former increased 150%, and in the latter 90%, during early anagen when compared with those of the telogen. From then on, both granular and spinous cells dropped rapidly even to "sub-normal" level when late anagen was reached. On the other hand the basal cells remained with little change throughout the whole cycle, but increased slightly (13%)

during early anagen and then returned to telogen at mid-anagen.

The results mentioned above were expressed by the following tables, and were counter-checked by whole mount studies of both epidermis and dermis.

From what had been observed in this study, it showed that the normal condition of mouse epidermis is not a "steady system" but changes according to hair follicular cycle, and the replacement of desquamating cells is carried out, most likely, by spinous cells instead of basal cells, as indicated by the constancy in the number of basal cells and the large fluctuation of spinous cells.

Table 1.
Nuclear Counts and Nuclear Diameter.

Stage or Time	Nuclear counts per $\overline{mm}^2$					Diameter (micron) of		
	basal cell nuclei	spinous cell nuclei	all inter-mitotic nuclei	granular cell nuclei	all nuclei	basal nuclei	spinous nuclei	granular nuclei
Telogen (control)	10,000	3,300	13,300	1,600	14,900	6.23	7.96	8.13
Anagen II (3 days)	11,300	6,300	17,600	4,000	21,600	6.84	8.08	8.44
Anagen IV (6 days)	10,600	4,900	15,500	3,000	18,500	6.77	8.01	8.05
Anagen VI (9 days)	10,200	4,200	14,400	2,000	16,400	6.43	7.44	7.85
Anagen VI (12 days)	9,500	3,400	12,900	1,600	14,500	6.80	8.15	8.39
Anagen VI (15 days)	9,700	2,500	12,200	1,500	13,700	6.45	7.77	8.25
Catagen (18 days)	9,800	2,900	12,700	1,400	14,100	6.35	8.02	8.23
Telogen (21 days)	10,100	3,300	13,400	1,600	15,000	6.17	7.86	8.05

Table 2.
Thickness (micron) of Epidermis.

Stage or Time	Intermitotic layer	Granular layer	Hornified layer	Whole epidermis
Telogen (control)	9.35	1.80	1.13	12.28
Anagen II (3 days)	17.51	8.12	5.43	31.06
Anagen IV (6 days)	13.20	4.04	3.50	20.74
Anagen VI (9 days)	11.72	2.63	2.96	17.31
Anagen VI (12 days)	9.88	2.41	2.42	14.71
Anagen VI (15 days)	8.30	1.61	1.57	11.48
Catagen (18 days)	8.68	1.56	1.35	11.59
Telogen (21 days)	9.38	1.93	1.19	12.50

DISCUSSION

A.G. SEARLE: What happens if you pluck hairs at the anagen rather than the telogen stage?

H.M. LIANG: Plucking of the club hair is to stimulate the growth of the new hair germs, while the hair germs have already been stimulated to grow through their natural cause, further plucking of club hair will cause little effect.

ZOOLOGICAL EXPLORATION OF NETHERLANDS NEW GUINEA

L. D. BRONGERSMA

Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

After Vasco da Gama discovered the sea route to the Indies in 1498, the Portuguese extended their voyages far to the east, and in 1511 they reached the Moluccas; they were soon followed by the Spaniards. In 1526 De Menezes visited some islands to the north of Geelvink Bay (probably the islands of Biak and Noemfoor), and in 1545 Ortiz de Retes reached the coast of the New Guinean mainland; in 1606 Luis Váez de Torres proved that New Guinea is an island. Dutch explorers also found their way to New Guinea, and sailing along the south coast in 1623 Carstensz sighted the snow-covered tops of the central mountain range. Many other voyages were made to New Guinea in the 17th and 18th centuries, but none of them was planned for scientific research. Nevertheless, the first information about the fauna reached Europe through these explorers, because they brought home specimens as souvenirs (e.g., the plumage of Birds of Paradise). It took many years before naturalists visited New Guinea or the adjacent islands. Sonnerat, the first of these naturalists, was evidently possessed of a lively imagination, which he displayed in a book published in 1776 entitled "Voyage à la Nouvelle Guinée". He did not reach New Guinea itself, but he visited the island of Gebe. From Papuans who crossed from Salawatti, he received a number of bird skins, and thus he could describe and figure various species unknown until then. Probably to add to the "value" of his book, Sonnerat included some birds that do not occur in New Guinea at all, viz., three specimens of penguins. It is due to this fraud that an Antarctic penguin has been named *Pygoscelis papua* Forster.

More serious research started in the 19th century. Several French expeditions visited New Guinea on their voyages, and one is still reminded of those taking part (Freycinet, D'Urville, Quoy & Gaimard, Hombron & Jacquinot) by many geographical, zoological, and botanical names. The first Dutch expedition to New Guinea in which naturalists took part visited the south coast in 1828 in H. Neth. M. corvette "Triton." In 1858 an expedition reconnoitred part of the south coast, and the north coast to Humboldt Bay. In later years C.B.H. von Rosenberg and H. A. Bernstein visited New Guinea and neighbouring islands to make zoological collections for the Rijksmuseum van Natuurlijke Historie at Leiden. Besides these collectors, who were in the service of the Netherlands Government, many travellers from other countries collected in New Guinea, viz., Alfred Russel Wallace, Beccari, D'Albertis, Meyer, Maindron, Raffray, Laglaise, etc. However, the exploration was limited mainly to the coastal areas.

The 20th century began with intensified activity, and a number of expeditions penetrated into the interior. In 1903 a Dutch expedition visited the north coast; three expeditions to the regions south of the central mountain range followed in 1907, 1909 - 1910, and 1913, and in 1920 - 1921 an expedition started from the north coast to penetrate to the Nassau Mts. and to Mt. Wilhelmina; a Netherlands-German border expedition took place in 1910. Two British expeditions visited the south in 1910 - 1911 (British Ornithologists' Union Expedition), and in 1912-1913 (Wollaston Expedition); a Netherlands-American expedition went to the Nassau Mts. in 1926. In all of these expeditions zoological collections were brought together which have proved very important in furthering our knowledge of the fauna. Moreover, the number of travellers individually made journeys to New Guinea, amongst others Miss L. E. Cheesman, who made important herpetological and entomological collections for the British Museum (Natural History).

In earlier days the problem of transportation was a handicap to all collectors. Where bearers had to be used, the equipment, and hence the collections, had to be limited. Better conditions were arrived at when air transport became available. The American-Netherlands Archbold expedition (1938 - 1939) made successful use of a flying boat. The expedition of the Royal Netherlands Geographical Society to the Wissel Lakes (1939) received transportation from the Royal Netherlands Naval Air Service, enabling it to bring extensive equipment into the field, and large collections were taken home.

The second world war stopped all scientific exploration in New Guinea, except that some members of the U.S. Forces made collections in the area. In 1948 the exploration was resumed when a Netherlands-Swedish expedition visited the island of Misool and the Vogelkop Peninsula. A number of traveller went individually to New Guinea; some of them to make collections for museums, others to obtain living Birds of Paradise for zoological gardens. The Swedish traveller Sten Bergman deserves special mention in this connexion for the interesting reports he has published on the courtship display of various species of Birds of Paradise; recently Bergman has succeeded in breeding King Birds of Paradise in captivity.

If we compare our present-day knowledge of the fauna of New Guinea to that of some sixty years ago, it is evident that much progress has been made, but it is equally clear that still more remains to be done. Aerial photography may fill up the large gaps once existing in our maps, but very large parts of the country have still to be explored from the ground. The central mountain range is difficult of access, and well-equipped expeditions will be necessary to penetrate into this part of the island. However, in many places in the lowlands and in the mountains the government and missionaries have settled, and these settlements offer good opportunities for individual collectors. The zoological exploration of the surroundings of these areas must not be delayed too long, because more and more of the land becomes cultivated, and this will greatly influence the composition of the fauna. Moreover, the zoological exploration may be of benefit to agriculture, fishery research, etc. With these arguments in mind the Rijksmuseum van Natuurlijke Historie, Leiden, made plans to intensify research by sending out zoologists, each of which a specialist in some groups of animals. It is important for the specialist to bring together the collections himself; he receives the specimens when they are still fresh, and the colours are not yet affected by drying or by preservation fluids; he may also be able to obtain information about the environment in which the species live, etc.

The first to visit Netherlands New Guinea under this scheme was the author of this report, who was sent out with one assistant in 1952. The funds for the voyage were provided by contributions from several scientific societies, private persons, and from industrial concerns. The full support of the Government of Netherlands New Guinea was obtained. Most liberal support was also given by the Royal Netherlands Navy. Only this help made it possible to visit many interesting places which the ordinary traveller never reaches from lack of transportation. Hospitality was also received from government officials and private persons. The main object was to assemble a collection of reptiles and amphibians, but attention was paid to other groups of animals as well. For a clear picture of geographical variability extensive series were needed from various localities, and the inhabitants did all they could to provide us with an ample supply. After a stay of about six months more than two thousand reptiles and amphibians were sent home for further study; particular attention was paid to the distribution and variability of poisonous snakes, the animals preyed upon, the number of young, etc. As this trip proved to be successful means and ways were sought for to continue the exploration in following years.

When the American forces occupied the islands of Biak and Owi towards the end of the Second World War, a great many cases of scrub typhus were reported. Although there was no such outbreak among the Netherlands forces that came to these islands, the possibility of a new outbreak remained. It was of vital interest to the medical service of the Royal Netherlands Navy to obtain data on the distribution of the mites (Trombiculidae) that carry the disease. Dr. L. van der Hammen, acarologist of the Leiden Museum, travelled to New Guinea for this purpose, and with full support of naval surgeons he studied various suspected areas. A report on the mites, their habitats, repellents, etc., was published in 1956. This research will have to be extended to a study of the animal hosts that serve as the scrub typhus reservoir. Dr. Van der Hammen also made extensive collections of Moss Mites (Oribatei), a group to which but little attention had been paid by previous collectors.

A further step was taken when the Government invited Dr. M. Boeseman to make a survey of the fish in several lakes and rivers (1954-1955). At the same time Dr. L. B. Holthuis travelled to Netherlands New Guinea to study the Crustacea of this region; the present author went out a second time to continue his studies on reptiles and amphibians; the trip was made possible by a grant from the Netherlands Organisation of Pure Research. Again the Royal Netherlands Navy gave liberal support both as regards hospitality and transportation. During a stay of about seven months many interesting places

were visited: the surroundings of Hollandia, Tami River, Lake Sentani, and the Nimboran area in the north-east of the Netherlands territory; the islands of Biak, Noemfoor, and Japen in Geelvink Bay; the Wissel Lakes in the Central Mountains; Ajamaroe, Aitinjo, and Manokwari in the Vogelkop Peninsula; Sorong and Misool Id. in the west; Fakfak in the south-west; Merauke and Tanah Merah in the south. About two thousand reptiles and amphibians, ten thousand fishes, and thirty thousand Crustacea were collected. The studies on the fish fauna by Dr. Boeseman, and those on Crustacea by Dr. Holthuis will help much to obtain a more complete picture of the composition of the freshwater fauna; these studies will also be of value to future fishery research, and hence to the food supply of the inhabitants. A remarkable feature of the fauna of New Guinea is the penetration of many marine forms into freshwater. This applies not only to the fish fauna (e.g., sharks in Lake Jamoer; Carangidae in Lake Sentani; etc.) but also to the sea-snakes. The sea-snake *Enhydrina schistosa* (Daud.) is fairly common in the Digoel River near Tanah Merah, 450 km. from the mouth of the river. Crayfish of the family Parastacidae occur only in freshwater basins that drain to the south; they are found in the central mountains (e.g., in the Wissel Lakes), in the southern lowlands, in the Vogelkop Peninsula (e. g., the lakes near Ajamaroe and Aitnijo), and on the island of Misool. Where fish are abundant (Lake Jamoer) Parastacidae are scarce, but in waters without fish (Wissel Lakes) or with a relatively poor fish fauna (lakes near Ajamaroe and Aitinjo, brooks flowing into Lake Jamoer) Parastacidae are abundant. To what extent crayfish and fish exclude one another will have to be studied in more detail, especially with regard to plans to introduce fish into waters where crayfish form as yet the only source of animal proteins for the local inhabitants (Wissel Lakes).

An agreeable consequence of the three trips made in recent years is the interest shown by persons living in New Guinea; several people have started collecting specimens for the museum, and many valuable data have been procured by them. In this way we received specimens of the strikingly coloured python (*Liasis boeleni* Brongersma) of the Wissel Lakes area, and recently photographs showed that the Longbeaked Spiny Ant-eater (*Zaglossus bruynii* Peters & Doria) occurs in this region. In 1910 M. Weber reported upon the occurrence of *Scleropages leichardti* Günther in the Digoel River; his report was based on a photograph received from Mr. J.M. Dumas; previously the species was known only from Queensland. Remarkably enough attempts made at the time to obtain specimens for further study all failed, and when Dr. Boeseman and I visited the Digoel River in 1955 we did not succeed in securing this fish. However, within a year's time two adult specimens and two juveniles reached our museum.

It is a long established fact that the fauna of New Guinea greatly resembles that of Australia, but that it differs widely from the fauna of Asia. This difference made a deep impression on the zoologists who in the 19th century travelled from Asia to New Guinea (e.g., S. Müller, A. R. Wallace), and many have been the discussions on the boundary between the Oriental and Australian regions of zoogeography. These problems do not need to be discussed here. Of more interest at the present time is the distribution of the fauna of New Guinea itself and of the adjacent islands. In 1936 Stresemann discussed the distribution of birds; this author showed that numerous species are represented by different subspecies north and south of the central mountains; sometimes the northern subspecies has penetrated to the west into the Vogelkop Peninsula, in other instances it is the southern subspecies that occurs there. The Crowned Pigeons (genus *Goura*) are represented by three species: one species in the Vogelkop Peninsula, one south of the mountains, and one north of the range. Little has been mentioned in literature about the distribution of reptiles and amphibians, although these groups also give evidence of the possibility of dividing Netherlands New Guinea into at least five faunal areas: the Vogelkop Peninsula in the west, the lowlands north of the central mountains, the lowlands south of the range, the area around Merauke in the south, and the central mountain range. The Vogelkop Peninsula Harbours several species of amphibians and reptiles that also occur in the Moluccas, but that are absent from the rest of New Guinea, e.g., the tree frog *Nyctimystes amboinensis* (Horst), the snake *Natrix elongata* (Jan), and the lizard *Hydrosaurus amboinensis* (Schloss.). The lowlands south of the mountains and the waters draining to the south coast harbour many species not found in the north, nor in the Vogelkop Peninsula, e.g., the freshwater turtle *Carettochelys insculpta* Ramsay, which occurs in Lake Jamoer and in the southern rivers (Setekwa River, Lorentz River, Digoel River, etc.). The snakes of the genus *Pseudechis* are only found in the south, and in the Netherlands

territory this probably also applies to the marsh tortoises of the genus *Chelodina*. Among the species of the genus *Emydura* this applies to *Emydura subglobosa* (Krefft), which is abundant at Lake Jamoer, and further to the south-east, e.g., at the Koembe River. This *Emydura* species is remarkable for its sloughing; the scutes of carapace and plastron peel off, several scutes together; moreover, this tortoise is noteworthy by producing a soft whistling sound (males only?). *Emydura novae-guineae* (Meyer) has a much wider distribution; it occurs north and south of the mountain range, in the Vogelkop Peninsula, and on the island of Waigeo. The area surrounding Merauke differs faunistically from the other lowlands. Here the Frilled Lizard (*Chlamydosaurus kingi* Gray) is found; the Death Adder is represented by a distinct subspecies, *Acanthophis antarcticus rugosus* Loveridge, and another snake (*Natrix Mairii* Gray) is represented by a form that comes close to that living in Australia. The absence of the Death Adder from the greater part of the Vogelkop Peninsula, and from the islands of Salawatti and Misool is interesting, as the species occurs farther to the west in the Moluccas (Ceram, Haruku, Obi). The New Guinean marsh crocodile (*Crocodylus novaeguineae* Schmidt) was described from the Sepik River in the Territory of New Guinea; later it was recorded from the neighbourhood of Port Moresby, and now it has been found in several localities in Netherlands New Guinea: Tami River, Lake Sentani, Lake Jamoer, and the Digoel River. Probably this species occurs in all lowlands, except in the Vogelkop Peninsula.

A matter of special interest is the forming of subspecies on the mainland of New Guinea, and on the adjacent islands. While all specimens of *Liasis amethistinus* (Schn.) from the mainland apparently belong to one and the same form, the island of Biak harbours a distinct subspecies, while other subspecies occur in the Moluccas, the Bismarck Archipelago, and in North Australia. The study of the subspecies in New Guinean reptiles is still in the initial stage, but the large series of many species recently acquired will offer possibilities for intensifying this part of research.

A continuation of the zoological exploration will make it possible to obtain a better picture of the distribution of many species, and of the faunal differences from area to area. The study of the habits of economically important species (e.g., of the crocodiles: *Crocodylus porosus* Schn. and *Crocodylus novae-guineae* Schmidt) is of importance to prevent extermination; measures have already been taken to protect these species to some effect, but more knowledge of the life history will enable the Government to make the protection more effective still. The study of species introduced into New Guinea (e.g., deer) is of importance as it may give us information about the deleterious effects of such introductions.

An important step to the further exploration of the central mountain range will be taken in 1958 when an expedition will go to the Star Mts., an area not yet visited by scientists. Various fields of research will be represented, among them zoology. This expedition will enlarge the knowledge of the mountain fauna obtained by two previous expedition in areas farther to the west (Wissel Lakes; Lake Habbema and Mt. Wilhelmina); it will be largely indepent of bearers, which use up much of the supplies they carry. An air-strip has been constructed in the valley of the River Sibil at 1200 m. above sea-level; this will make it possible to fly in personnel and supplies, and to take out large collections. Exploration groups will proceed into the mountains on foot, but they will be supplied from the air by helicopter.

The remarkable fauna, and the great diversity in environment make New Guinea an ideal country for zoological research. It reaches from the hot tropical lowlands to the snow-covered mountains, from areas with a well marked dry season and with a relatively low annual rainfall (Merauke, 1530 mm.) to places with an annual rainfall of 6434 mm. (Ninati at the southern foot of the mountains), from dense forests to open grasslands and tree-less mountains. This diversity in climate and vegetation brings along a diversity of the fauna well worth studying.

DISCUSSION

Dr. Taylor asked how Dr. Brongersma was able to obtain the use of three modern ram jet helicopters for this expedition. Dr. Brongersma replied that the navy and private concerns were interested in this work for various reasons, and underwrote the cost. Further, knowing the right naval officers facilitated matters greatly.

Dr. Mead asked about the personal dangers of canabalistic local inhabitants. Dr. borngersma said that while such danger exists, his own experiences proved the local inhabitants pleasant, friendly and amused, and quite willing to barter specimens for fish hooks and razor blades.

GEOGRAPHY AND SYSTEMATIC RESEARCH†

EUGENE MUNROE

Principal Entomologist, Insects Systematics and Biological Control Unit, Ottawa, Canada.

The importance of geography in the subject matter of systematics is well known, and I do not propose to discuss it here. This paper deals with the practical effects of geography on systematic research, a subject on which I have formed some opinions in the course of a number of years of work on a variety of faunas.

Geography affects the planning of systematic research in several ways. These depend basically on the spatial and political relations of the worker to the habitats of the groups he wishes to study, to the sites of important collections, including those in which type specimens are housed, and of libraries and working facilities, and to sources of financial support for the work.

From many standpoints the simplest kind of taxonomic project to organize is the local, faunistic one. Worker, facilities, funds and fauna are all in close proximity and problems of finance and transport are consequently minimized. It is not surprising that the great majority of projects actually undertaken are of this type. Even here, however, geographic problems arise. Faunistic work is geographically concentrated, but the tendency is for larger groups to be studied, so that the taxonomic knowledge of the worker tends to be attenuated. He is consequently at the mercy of outside specialists or of his own incomplete knowledge for correlation with other faunas and the broader taxonomic framework of each group. Years ago Rothschild and Jordan in their comprehensive studies of swallowtail butterflies noted that the existence of local lists was often more of a hindrance than a help, because of the constant necessity for checking out-of-date identifications from a variety of sources, often inadequately correlated by the non-specialist author. Correspondence with specialist identifiers involves the difficulty of locating suitable specialists to begin with, and of keeping abreast with and harmonizing their divergent views. In many groups careful faunistic work necessarily involves the study of foreign collections, either because important collections of the fauna are kept in foreign institutions, or because the type specimens of many of the species are in foreign countries. In such cases the student must travel abroad even if the fauna of the country concerned is not directly related to the one he is studying.

With a primarily taxonomic rather than faunistic approach, projects tend to become global in scope. Practical geographic problems become acute, though this is somewhat offset by the technical advantages inherent in a balanced study. It is not surprising that projects of this kind have always been in the minority. Unfortunately, the proportion has tended to decrease with the modern decrease in private or independent sources of support. The practical obstacles in the way of work on a group from a world-wide standpoint are obvious. First, the assembly of material presents formidable problems. Specimens can be bought from some places, exchanged from others, and borrowed from yet others; these sources can sometimes be supplemented by expeditions to regions of particular interest. However, most of these arrangements are costly and all are time-consuming. The most important difficulty in the assembly of really representative material is not money—even a modest annual expenditure over a long period of time will bring surprising returns—or the generosity and patience of collectors and curators—both are very great—but the sheer expenditure of time in correspondence, and in labellings, preparing, arranging, packing and shipping specimens. Secondly, even when large collections have been assembled and satisfactory taxonomic concepts have been formed, the correct application of names requires the examination of type specimens, which may be scattered in a variety of collections in a number of countries. To a large and increasing extent types are being immobilized by institutional policy. It is of course possible, if time and money are available, to go to see types, but even so one must depend on notes, sketches or photographs, and it is impossible to examine the types in conjunction with the representative series which may have taken so much time to collect. Thirdly, funds for the prosecution and publication of large taxonomic studies nowadays come to an increasing extent from governmental sources,

† Contribution No. 3773, Entomology Division, Science Service, Canada Department of Agriculture.

and governments tend to be interested primarily in work applicable directly within the political boundaries under their jurisdiction. Work of broader scope has less immediate appeal to them, and is correspondingly harder to initiate or justify.

I think it will be agreed that in spite of these practical disadvantages the broad taxonomic study is a desirable and indeed an essential complement to the narrow faunistic one. Systematists have therefore a responsibility to undertake constructive measures to overcome the difficulties in its way. Problems of material, though important, are perhaps in general the easiest to overcome. For almost all broad taxonomic projects there is already in collections an abundance of material if only it can be assembled—it is the specialized geographic or microtaxonomic study that is likely to need material in excess of the available supply. The co-operation of colleagues is very readily obtained, and it is only rarely that unrealistic individual or institutional policies stand in the way of the assembly of material for worthwhile studies.

A curious phenomenon that sometimes interferes with the free flow of material, one that is in a way symptomatic of our times, is what may be called taxonomic nationalism. This is the view that the fauna of a particular political area should be preseved for collection or even for study by nationals of that area. I think it is fair to say that this restrictive attitude seems to be most prevalent in countries where taxonomic work has for one reason or another lagged in the past and where a rising generation of active workers views with regret the time and opportunities that have been lost. I can say this without prejudice as my own country has not always been free of taxonomic nationalism. Although the local concentration of material pertaining to a geographic area is a valuable and desirable thing, this should be brought about by positive and flexible means, not by negative and rigid ones. The overall scientific objective must always be to increase the amount and availability of human knowledge. Attempts to secure local advantage by the restriction of information and facilities almost always result in more loss than gain, because of the general slowing of progress in the field of research concerned, and because purely local studies must invariably contain elements of error and bias that could be eliminated by taking a broader basis or by consultation and collaboration with outsiders.

Taxonomic nationalism often means that collections are preserved in places inconvenient from the standpoint of the main centres of research on the groups concerned, or indeed from the standpoint of safe preservation over long periods of time. Indeed the location of collections presents very special problems, not wholly bound up with nationalism. It is true that almost any place, whatever its climate, can by the aid of modern techniques be made safe for the preservation of specimens. In unfavourable climates, however, especially in the wet tropics, safety requires much more rigid and frequent measures of inspection and prevention than it does in more moderate environments. In such places periods of neglect—to which no collection is absolutely immune—can have extremely serious consequences, consequences which might well be escaped in a dry and temperate location. Other factors than climate must be taken into account: the risk of fire, earthquake and eruption must be considered, as well as that arising from war or civil disturbance. Recent examples of destruction or major damage show that none of these risks can safely be ignored. A disturbingly large proportion of major biological collections are located in the central parts of capital or industrial cities. How many of them could be evacuated to safety in the event of a major catastrophe such as a fire or the sudden cutbreak of modern war? Many of these risks could be minimized by suitable geographic location.

The considerations that apply to the location of ordinary collections apply with redoubled force to the location of type specimens. It goes without saying that types ought to be kept in the safest possible location consistent with convenience of use. The two primary considerations, safety and convenience, are unfortunately to some extent opposed. This is particularly so in the problem of whether or not types shall be loaned. On the one hand a type is a unique standard, though not necessarily an irreplaceable one, now that the neotype is a recognized category, and there is a natural reluctance to expose it to the risks of shipment. On the other hand no location, however carefully chosen, can be convenient for all the workers likely to be interested in a given type, or even for a majority of them. As already noted, travel even when a possible solution is not always a complete one. There is little doubt that the inaccessibility of types is one of the major obstacles to taxonomic progress to-day, and the obvious answer is that the rigid immobilization of types as an invariable policy is

wrong. No one would advocate the reckless shipping of types hither and thither on the slightest pretext and regardless of caution. On the contrary, every sensible person would want to minimize their movement. However, this is a very different thing from keeping them from moving at all. The loan of types to responsible individuals in deserving cases and with due attention to safety in transit is in my opinion a very desirable thing; to oppose it is to take a ritualistic view of an essentially practical problem. What constitutes safety in transit is a debatable matter, almost as hard to define as what constitutes safe preservation in a museum. Possibly a system of personal carriage of types by entomologists known to be travelling in the desired direction could be established as a regular custom.

The third of the major problems mentioned above, the availability of funds for work of world-wide or international scope, has become acute in recent years with the decline of private fortunes and endowments and the increasing importance of government support. Even some large private institutions have, in the face of shrinking funds, tended to confine their interests to limited geographic areas, and this has almost been the rule with government museums. Counteracting this tendency are two favourable factors—the activities of the major research foundations, several of which have supported broad taxonomic work, and the increased realization of government departments that fundamental studies must receive their fair share of attention if more immediately applicable projects are to prosper. It may be hoped that these good tendencies will prevail, and that taxonomy will not lapse into an ineffective provincialism.

DISCUSSION

Dr. Mead wondered whether in view of the concept of species as a population and might eventually come to depend more on type localities rather than type species, and merely go to the locality and obtain samples of the population under consideration.

Dr. Munroe pointed out that populations change, hence such a plan is unfeasible. Further, several closely related populations in one area would make it impossible to be certain one was sampling the right population.

Dr. Cowan cited the extirpation of one species of wolves in Canada and their replacement by another species, a situation which would certainly negate Dr. Mead's proposition. Further, "explosive populations" occurring at the time either of citing a type locality or at time of subsequent collection would add to the misrepresentation of such a sampling.

Dr. Brongersma predicted that systematists would have to continue to inspect type collections and tolerate all the inconveniences entailed.

COMPARATIVE RESEARCH OF BIOLOGY OF THE LITTORAL IN THE FAR EASTERN SEAS

EUPRAXIE GURJANOVA

The Zoological Institute, Academy of Sciences of the USSR, and the Leningrad University, Leningrad, U.S.S.R.

A comparative research of biology of the sea-shore from the Barents sea to the Siberian seas in the Arctic and from the Berings Strait to the Korean peninsula in the Far-Eastern seas as well as in the Black sea and in the eastern part of the Baltic sea has been carried out during last 30 years by the Soviet scientists. Last summer the area of these explorations was extended further to the South in the Yellow sea by the joint expedition of the Zoological Institute of the USSR and the Institute of Marine Biology of the Academia Sinica (Tsing Tao). All that enables us to formulate some general principles of the researches within the limits of the intertidal zone and to make some bionomic and biogeographical conclusions. Our researches were based on the following basic ideas.

1. Within sea-shore there are two zones situated above the lowest level of sea-Supralittoral and Littoral. Both are the independent zones of the ocean as they possess special conditions of life and a specific composition of fauna and flora; both of them greatly differ from other vertical subdivisions of sea or zones.
2. The limits of Supralittoral are determined by the highest level of flood (lower limit) and by the bound of penetration of splash of waves (upper limit). There are land-conditions of life, but the irregular wetting of shore with sea-water creates some specific biotops where both land (some plants, Insectes, Myriapoda, Mollusca, Arachnoiden) and marine organisms (algae, Crustacea, Mollusca and even fishes) find some favorable habitation.
3. The limits of Littoral are determined by the maximum of theoretically possible level of high waters (upper limit) and by the level of maximum low waters or zero of depth used on the Soviet sea maps (lower limit). The daily regular uncovering creates here very specific amphibiotic conditions of life.
4. The life of Littoral is subordinate to the rhythm of tides. All the factors of surroundings (t^0, salinity, light etc.) and especially the regular interchange of water-and air-conditions have diurnal fluctuations which depend on daily fluctuations of sea-level. Natural biological phenomena within this zone must be subordinate to this rhythm too (the time of spawning, the vertical migrations in soft ground of some verms and Bivalvia, hunting and nutrition of animals and the intensity of photosynthesis of algae and sea-plants etc.).
5. The periodicity of all these changes depends on the type of tides which is characteristic of each region of sea-shore.
6. Within littoral zone we can observe a regular change of life conditions in vertical direction from the upper limit down to the lower one. Correspondingly we can see a clear vertical stratification of species and communities, each of them has its own place located at a definite level above zero depth and ordinarily forms some kind of belts (in conditions of arctic and boreal climatic zones) or mosaic (in conditions of south-boreal and subtropic zones).

As our experiments show the vertical stratification of the littoral species depends on their capacity to bear fading and large rising heating or falling (freezing) of temperature.

7. Zones and their upper and lower limits at each sea-shore area remain constant. As it is shown by K. Derjugin, 1928, zones and their vertical subdivisions do not change their places relative to zero depth. On the contrary, species and communities move within their zones up or down under the influence of changing of some definite factors of surroundings, and even can move from one zone to another.
8. If specific composition of fauna and flora is determined by some geographical and historical factors (climate, paleogeography and origin and history of formation of fauna and flora of the region), the allotment of species and communities depends upon the present ecological conditions within the region.

9. At first changes of surrounding conditions lead to change in vertical distribution of littoral species and communities but the specific composition of fauna and flora remains the same. We can observe on a sea-shore with normal salinity (33-35°/oo) and calm water a normal stratification of communities which is typical for every geographical region. The whole system of communities rises up at exposed coasts and descends lower in brakish waters without breaking the order of their vertical zonation; rapid streams mixed communities together and their sharp stratification fades away.

Thus the stratification of species and communities is more sensible than their specific composition and it indicates best of all the changing of conditions in comparison with the mean standard. In this way to be able to notice these kinds of bionomic change we must have some constant coordinates for comparison. Thus, the principle of vertical subdivision of intertidal zone which we consider to be a basic one has the most important significance in cognition of the regularities of littoral life.

There are two kinds of subdivision of littoral zone into subzones, horizons, stories etc. Some authors use Vaillant's principle, which was applied by him to the North Atlantic coasts characterised by regular semidiurnal tides (Vaillant, 1891). According to Vaillant, the limits of each of his three horizons are connected by definite sea-levels (Table I). That system was successfully applied to the Littoral of the Murman coast, White sea and Spitzbergen by Herzenstein, 1885, Knipowitsch, 1891, 1906 and Birula, 1894, 1896, 1898, 1906 and to the different areas of the Russian northern and far-eastern seas by Soviet authors (Gurjanova, 1935-1949; Gurjanova, Zachs, Ushakov, 1925-1930; Gurjanova, Ushakov, 1925-1930; Ushakov, 1949, 1951; Kussakin, 1956 etc.). Other scientists use Stephenson's biological principle (T.A. Stephenson and A. Stephensen, 1949) and subdivide the Littoral into subzones according to the distribution of species.

They do not take into consideration that a very close connection exists between vertical limits of the distribution of species and tidal sea-levels. The latter principle was subjected to a just criticism. To our mind this principle cannot be used in comparative bionomic study of intertidal zone without the help of the Vaillant's system of horizons, the limits of which are quite impersonal and exact. Besides, these limits are at the same time the critical levels of the major part of the littoral species; it is only not quite clear for us whether the mean sea-levels during the different phases of tides or the highest and

Table I
Regular Semidiurnal Tides
(Barents sea)

$$\frac{H_{k_1} + H_{o_1}}{H_{m_2}} = 0.0$$

The highest level of High-waters of Spring-tides.

VAILLANT'S HORIZONS OF LITTORAL ZONE	I HORIZON	Exposed to air during Neap-tides. Covered with water twice per day during Spring-tides. Mean level of High-waters of Neap-tides.
	II HORIZON	Covered with water and exposed to air twice per day, every day during Neap—and Spring-tides. Mean level of Low-waters of Neap-tides.
	III HORIZON	Covered with water during Neap-tides. Exposed to air twice per day during Spring-tides. The lowest level of Low-waters of Spring-tides. (Zero depth).

the lowest ones coincide with the critical levels of littoral animals and plants the nearest.

Researches carried out by the Soviet scientists show that the vertical distribution or stratification of littoral species and communities does not depend on the angle of bottom slope; the latter determines only the degree of development of the communities (Nordgaard's rule) and belts of species became wider or narrower with changing of this angle.

The influence of amplitude of tidal fluctuations of sea-level is of the same kind: it determines only the space occupied by each of species or communities but does not change their zonation. Only in one case the vertical distribution of species and communities does not depend on the tidal fluctuations of sea-level—it is observed when the amplitude of these fluctuations (the range of tide) is smaller than changes of sea-level caused by winds. These conditions we can find in the Black, Azov and Baltic seas and in the Peter the Great Gulf (Japan sea). In all these cases the Soviet scientists use a new term "Pseudolittoral" zone (Mokijevsky, 1956).

The comparative research of sea-shore of the north-western part of Pacific is especially interesting for there we can observe different types and different ranges of tides from 0.5 m to 13 m in different areas; it is especially interesting too for the coast-line passes through all four climatic zones of the northern hemisphere—arctic, boreal subtropic and tropic ones without interruption and a permanent free exchange of fauna and flora can take place along the coast of Asia.

As shown by our researches the Vaillant's principle of subdividing the intertidal zone can be applied not only to the sea-shore with regular semidiurnal tides, but to the places with other types of tides, i.e. with regular (Hon-Daw, Southern Chinese sea) and irregular diurnal (Petropavlovsk-Kamschatka, Kommander islands) and irregular semidiurnal tides as well (Soviet Harbour—Japanese sea, Nagaeva bay, Taujsky bay—Okhotsk sea). In all these three latter cases there are three horizons similar to those established by Vaillant. For each of them there are limits corresponding to mean levels of tropical and equidiurnal tides in places with regular and irregular diurnal tides as well as to mean levels of spring-and neap-waters in places with irregular semidiurnal tides. In cases of irregular tides there exist some additional limits, which divide horizons into stories (Tables II-IV); some special cases of irregular diurnal tides and of "shallow-water" tides are shown in Tables V and VI.

The most complex cases of rhythm of life are observed within the places with irregular semidiurnal tides, because the latter can be of three different kinds:

Table II

Regular Diurnal Tides

$$\frac{H_k + H_0}{H_{m_2}} = 2.5.$$

The highest level of High-waters of Tropic-tides.

HORIZONS OF LITTORAL ZONE	I HORIZON	Exposed to air during Equidiurnal tides. Covered with water once per day during Tropic-tides. Mean level of High-waters of Equidiurnal-tides.
	II HORIZON	Exposed to air and covered with water once per day during both Equidiurnal and Tropic-tides. Mean level of Low-waters of Equidiurnal-tides.
	III HORIZON	Covered with water during Equidiurnal tides. Exposed to air once per day during Tropic-tides. The lowest level of Low-waters of Tropic-tides. (Zero depth).

Table III

Irregular Semidiurnal Tides $\frac{H_{k_1} + H_{o_1}}{H_{m_2}} = 0.5$, but 2.0.

The highest level of High-waters of Spring-tides.

HORIZONS OF LITTORAL ZONE	I HORIZON	Exposed to air during whole period of Neap-tides. Covered with water once or twice per day during Spring-tides. Mean level of high High-waters of Neap-tides.
	II HORIZON	Exposed to air and covered with water every day once or twice per day during both Spring — and Neap-tides. Mean level of low Low-waters of Neap-tides.
	III HORIZON	Covered with water during Neap-tides. Exposed to air once or twice per day during Spring-tides. The lowest level of low Low-waters of Spring-tides (Zero depth).

Table IV

Irregular Diurnal Tides $\frac{H_{k_1} + H_{o_1}}{H_{m_2}} = 2.0$, but 4.0.

The highest level of High-waters of Tropic-tides.

HORIZONS OF LITTORAL ZONE	I HORIZON	Exposed to air during Equidiurnal tides. Covered with water once per day during Tropic tides. Mean level of High-waters of Equidiurnal-tides.
	II HORIZON	Exposed to air and covered with water twice per day during Equidiurnal tides and once per day during Tropic-tides. Mean level of Low-waters of Equidiurnal-tides.
	III HORIZON	Covered with water during Equidiurnal tides. Exposed to air once per day during Tropic-tides. The lowest level of Low-waters of Tropic-tides (Zero depth).

1. The diurnal inequality is observed between adjoining (neighbouring) both high- and low-waters (Gongcong, Singapore, San Francisco, Freaser River etc.).
2. The diurnal inequality takes place between adjoining highwaters only, but the neighbouring low-water have almost the same height (Soviet Harbour—Japan sea, Shanhaj, Honolulu etc.).
3. The diurnal inequality is characteristic only for adjoining low-waters, but between neighbouring high-waters there is no difference (Nagaeva bay, Okhotsk sea etc.).

In the first case the semidiurnal rhythm there is only within the horizon of Littoral; both first and third horizons have a diurnal rhythm. Water covers the first horizon once per day during the whole lunar-month; the lower limit of this horizon is the mean spring low-high-waters level; here there are two stories—upper one which is covered with water once per day only during spring-tides,

Table V

A Specific Case of Irregular Diurnal Tides (Kommander Islands)*

$$\frac{H_{k_1} + H_{o_1}}{H_{m_2}} = 2.53$$

The highest level of High-water of Tropic-tides.

HORIZONS OF LITTORAL ZONE	I HORIZON			Exposed to air during equidiurnal tides; covered with water once per day during tropic tides. Mean level of high High-waters of Equidiurnal-tides.
	II HORIZON	STORIES OF II HORIZON	1 STORY	Covered by water and exposed to air once per day during tropic tides and twice per day during Equidiurnal tides. Mean level of high Low-waters of Equidiurnal-tides.
			2 STORY	Covered by water and exposed to air once per day during the whole lunar month. Mean level of low Low-waters of Equidiurnal-tides.
	III HORIZON	STORIES OF III HORIZON	1 STORY	Exposed to air once per day during tropic-tides. Covered with water during Equidiurnal-tides. Mean level of low Low-water of Tropic-tides.
			2 STORY	Covered with water during Equidiurnal and ordinary Tropic-tides; exposed to air once per day during "large" tropic-tides in Spring time. The lowest level of Low-waters of Tropic tides in Spring-time.

* Tides within the Kommander islands are of the same type as within the eastern coast of Kamtschatka (Petropavlovsk), i.e. irregular diurnal ones; but they have some specific features:

1. A large diurnal inequality of adjoining low waters of semidiurnal equidiurnal tides;
2. A considerable difference of heights between high waters of tropic and equidiurnal tides;
3. The existence of some "large" low waters, which are very rare and take place almost exclusively in Spring time (March-April).

and the lower one which is covered with water once a day during both spring-and neap-tides. The second horizon has a semidiurnal rhythm, but is clearly divided into three stories—upper one has a semidiurnal rhythm only during spring-tides as both adjoining high-waters cover it, but during neap-tides period it is covered once per day by high-waters only. Second or middle story has a semidiurnal exchange of air and water conditions every day; the lower story is analogous to the upper one as it has a diurnal rhythm during neap-tides and a semidiurnal rhythm during the

Table VI

"Shallow-Water" Tides Within the coasts of the Shandunsky Peninsula, Yellow Sea
Regular semidiurnal tides.

$$\frac{H_{k_1} + H_{o_1}}{H_{m_2}} = 0.38$$

The highest level of High-waters of Spring-tides*

HORIZONS OF LITTORAL ZONE	I HORIZON			Exposed to air during Neap-tides. Covered with water once per day during Spring-tides. Mean level of low High-waters of Spring-tides—high High-waters of Neap-tides.
	II HORIZON	STORIES OF II RORIZOHN	1	Covered with water once per day during Neap-tides and twice per day during Spring-tides. Mean level of low High-water of Neap-tides.
			2	Covered by water and exposed to air twice per day during whole lunar month. Mean level of high Low-water of Neap-tides.
			3	Exposed to air once per day during Neap-tides and twice per day during Spring-tides. Mean level of low Low-waters of Neap-tides.
	III HORIZON	STRORIES OF III HORIZON	1	Covered with water during Neap-tides; exposed to air twice per day during Spring-tides. Mean level of high Low-waters of Spring-tides.
			2	Covered with water during Neap-tides and ordinary Spring-tides; exposed to air rarely during "large" Low-water of Spring-tides. The lowest level of low Low-water of Spring-tides.

* Here as well as within the Kommander islands some very "Large", but rare ebbs occur generally in winter. Tides have the semidiurnal rhythm, but there is a considerable diurnal inequality of adjoining low waters; the heights of adjoining high waters are epual; a coinciding of low high water of Spring-tides and high High-waters of Neap-tides takes place here.

Table VII.

Vertical Distribution of Animals within the Muddy Beach Tsan-kow near Tsing Tao (Yellow Sea, Southern Coast of Shandunsky Peninsula). Subtropic Geographical Zone.

(After E. Gurjanova, Y. Liu, O.Scarlato, T. Tsi and P. Ushakov, 1957)

4.5 m	SUPRALITTORAL ZONE	No animals or plants				4.5 m
	LITTORAL ZONE	I HORIZON	1 STORY	Helice tridens (many specimens)	Sesarma sp. (under gravel and small stones)	4.1 m
3.6 m			2 STORY		Scopimera globosa (few specimens)	3.6 m
		II HORIZON	1 STORY	Scopimera globosa (many specimens)	Perenereis nuntia v.brevicirrus Audouinia sp. Lingula anatina juv. (few specimens)	2.9 m
			2 STORY	Macrophthalmus japonicus and Lingula anatina	Perenereis sp.; Audouinia sp.; Glycera sp.; Platinereis sp.; Alpheus sp. many; Solen gouldi many; Bullacta exarata; Hemigrapsus penicillatus many; Scopimera globosa (few); Diapatra neapolitana; Lumbriconereis sp.; Upogebia major (few specimens and very deep in mud).	2.0 m
1.6 m			3 STORY	Upogebia major (a great many) and Gavernularia sp.	Mactra quadrangularis; Dosinia sp.; Dosinia japonica; Venerupis philippinarum; Solen gouldi; Vivariegatas; Hima sp.; Anatina peckohiliensis; Thalassema sp.; Morphysa sp.; Diopatra neapolitana; Lumbriconereis sp.; Amphiura valida; Alpheus No.2 and others.	1.6 m
		III HORIZON	1 STORY	Macrophthalmus dilatatus (a great many)	Philine kinglipini; Alectrion variceferus; Dosinia japonica; Solen gouldi; Mactra sp.; M. quadrangularis; Amphiura valida; Venerupis variegatus; Armandia sp. Pota milla sp.; Balanoglossus; Callianassa 2 species; Pilyra carinata etc.	0.5 m
			2 STORY	Upogebia wusienweni and Lingula sp. No. 2	Branchiostoma belcheri var. tsingtaoensis ; Matata planipes; Oryphia maculata and some sublittoral species.	(Zero depth) 0 m (datum)

Table VIII.

Vertical Distribution of Species and Communities within the Rocky Beach near Nikolskoje (Berings Isle, Kommander Islands).

Irregular diurnal tides. Temperate geographic zone
(After E. Gurjanova, 1930-1931)

5 m							Limit of splash 5 m
5 m – 4 m	SUPRALITTORAL ZONE	I HORIZON				Plants and animals. Lathyrus maritimus; Mertensia maritima; Ligusticum scoticum; SAND AND GRAVEL	larvae of Coleoptera and Diptera; Myriapoda; Machilis sp.; Turbonilla sp.; Helix sp.; Arachnoidea; Allorchestes wladimiri; Orchestia trinitatis; limit of surf-washing 4 m
4 m – 3.26	SUPRALITTORAL ZONE	II HORIZON				Only animals. Orchestia trinitatis; Allorchestes wladimiri; Anisogammarus locustoides; Echinogammarus ochotensis; Detonella papillicornis; Halobesiumorientale; Staphilinidae; Oligochaeta; Littorina sithana(few). SAND AND STONES	3.26 m
3.26 – 3 m	LITTORAL ZONE	I HORIZON	1 STORY			Littorina sithana (many)	Green algae, Uropora and Prasiola in Spring. Bangia fuscopurpurea + 2 species of Gleiopeltis in Summer. 3.0 m
3 m – 2.46	LITTORAL ZONE	I HORIZON	2 STORY			Littorina sithana + Acmaea No. 1	Belt of Diatomacea (Melosira sp.) in Spring. In Summer algae are absent. 2.46 m
2.46 – 2 m	LITTORAL ZONE	II HORIZON	1 STORY			Acmaea No. 1. Littorina sithana Echinogammarus sp. Gammarus sp.	Belt of Porphyra and Diploderma in Spring. Belt of Gloiopeltis furcata in Summer. Fucus evanescens whole year. 2.00 m
2 m – 1.20	LITTORAL ZONE	II HORIZON	2 STORY	Fucus evanescens and Mytilus edulis			L. sithana; Acmaea No. 2; several species of Gammaridae; Lineus sp.; small Polychaeta; Acmaea No. 1; Ischnochiton ruber; Pagurus hirsutiusculus; Janiropsis kincaidi.
	LITTORAL ZONE	II HORIZON	2 STORY	Fucus evanescens and Mytilus edulis		Odonthalia floccosa coniosa	Phiscosoma japonica; Thais lima; Acmaea No. 2; Acmaea No. 3; Pagurus hirsutiusculus; P. middendorfi; Cucumaria vegae juv. very many in Spring.
	LITTORAL ZONE	II HORIZON	2 STORY	Fucus evanescens and Mytilus edulis		Fucus inflatus and Rhodymenia palmata	Alaria sp. (rare); Idothea allutica; Chiton 2 species; Pagurus hirsutiusculus; P. middendorfi; P. gilli; Hapalogaster grebnitzkii; Dermaturus brandti; very rich fauna of Gammarids and Polychaeta. 1.20 m
1.20 – 1 m	LITTORAL ZONE	III HORIZON	1 STORY	SEMIBALANUS CARIOSUS		Laminaria nigripes Laminaria longipes Haedophyllum sp. Corallina Halichondria Alcyonidium cervicornis	Very rich fauna of Crustacea, vermes and Mollusca; Pagurus middendorfii; P. galli; Hapologaster grebnitzkii; Dermaturus mandti: Paralithodes brevipes juv.; Cheiragonus cheiragonus; Leptasterias 2 species. 1.00 m
1 m – 0.60	LITTORAL ZONE	III HORIZON	1 STORY	SEMIBALANUS CARIOSUS	SPIRORBIS SEMIDENTATUS; LITHOTHAMNIUM SP.	Laminaria dentigera Amphiroa cretacea Schizobranchus insignis	Pagurus gilli; P. undosus; Hapalogaster Amphineura 5 species; Leptasterias 2 species; and Dermaturus; Paralibrotus brevipes juv.; Strongylocentrotus 2 species; Cheiragonus; Oregonia gracilis; very rich fauna of Polychaeta, Amphipoda, Mollusca, Nemertini. 0.60 m
0.60 – 0 m	LITTORAL ZONE	III HORIZON	2 STORY:	SEMIBALANUS CARIOSUS	SPIRORBIS SEMIDENTATUS; LITHOTHAMNIUM SP.	Thalassiophyllum clathrum + Spongia, Synascidiae, Bryozoa on the thallus.	Rich fauna of sessile animals; Leptasterias 2 species; Henricia several species; Strongylocentrotus 2 species; Schizoplax brandti; Cryptochiton stelleri and other species of Amphineura; Monia macroschisma; Hapalogaster, Dermaturus, Paralithodes brevipes, Oregonia gracilis, Pugettia quadridens; several species of fishes; the richest fauna of Mollusca, Polychaeta, Amphipoda and Isopoda. (Zero depth)
0 m							

period of spring-tides. The upper limit of the third horizon (and the lower limit of the second one) is the mean high low-waters level of neap-tides.

In the second case the first horizon of Littoral is very short in vertical direction because its lower limit is the mean high-waters level of spring tides; this horizon is covered with water only during spring-tides and has a semidiurnal rhythm as the adjoining high-waters have almost the same height. The sccond (middle) horizon has a semidiurnal rhythm during the whole lunar-month as its lower limit is the mean high low-water level of spring-tides. This horizon is divided into two stories — the upper one has always a semidiurnal rhythm; the lower story during neap-tides has a diurnal rhythm but a semidiurnal one is observed only during spring-tides. The third horizon has always a diurnal rhythm and is divided into two stories — the upper one exposed to air every day once a day, the lower one exposed to air once a day only during spring-tides.

In the third case when the diurnal inequality takes place between adjoining high-waters only, the first horizon has always a diurnal rhythm as the lower limit of it is the mean low high-water level of spring-tides. This horizon has two stories — the first one is covered with water only once a day during spring-tides, the second one is covered with water once a day every day during lunar month.

The second (middle) horizon has a semidiurnal rhythm and is divided into two stories too — the first one has a semidiurnal rhythm during spring-tides only, the second one has such a rhythm during the whole lunar month, as the lower limit of the horizon (= upper limit of the third horizon) is the mean low water level of neap-tides. The third horizon is exposed to air only during spring-tides and as both adjoining low waters have no difference in their heights, this horizon has a semidiurnal rhythm.

Some specific rhythm of life is characteristic in conditions of "shallow-water" tides. An example of it is shown in Table VI. Within Shandunsky peninsula tides are regular semidiurnal (see the formula of them); but very small depth of Yellow sea caused out some special deformation of tides: as result the first horizon has a diurnal rhythm, the second (middle) horizon is divided into three stories and each of them has its own rhythm of life; the thrid (lower) horizon is divided into two stories and each of them has its own rhythm too (Table VI).

The difference of tides rhythm within different parts of amphibiotic littoral zone show the necessity of subdividing this zone into horizons and stories according to Vaillant's principle; without it we can not catch regularities of littoral life and will not understand the causal dependency between biological phenomena and their surroundings.

We have many practical Tables illustrating the vertical distribution of communities and their specific composition as well as absolute position of their limits above datum (zero of depth) (Gurjanova E.F., 1924-1949; Gurjanova E., Ushakov P., 1928-1925; Gurjanova E., Zachs J., Ushakov P., 1925-1930 etc.); in these Tables the limits of horizons and their stories are shown too. As examples I would like to show only two such Tables (Tables VII and VIII); they both reflect the natural distribution of species within the place with mean normal conditions. Having such Tables made by researchers for every place visited by them it is possible to compare directly littoral zones of different seas and climatic zones and make some bionomic and biogeographical conclusions.

If zonation proposed by Stephenson can be applied to rocky beaches only, the zonation based on Vaillant's principle can be used for different kinds of beaches—rocky, stony, sandy, muddy-beach etc.

The most specific feature of the Far-Eastern seas in comparison with Atlantic coasts is the existence of two datums (zeros of depth). This phenomenon depends on the monsoon climate and the periodical law of Tsusima current out-go. At the western coast of the Japan sea, for example, zero of depth in winter lies lower than in summer by 30-45 cm.

Thus we have here an additional specific intermediate horizon between littoral and sublittoral zones covered with water during the whole summer and exposed to air during ebbs only in winter (from October to April), when the mean sea level is lower. In such a way within the lower part of Littoral a semiannual rhythm of life exists here besides diurnal or semidiurnal one. Adaptations of sea-shore species to these specific conditions had stipulated the existence at the western coast of Japan sea of fauna and flora spreaded from the middle part of Littoral to the depth of 15 m, i.e. the most part of the sea-shore species here is adapted to conditions not only of intertidal zone but to conditions of sublittoral too.

When examining our materials we came across many general and specific bionomic regularities (see our articles).

As the coastal line of the USSR is an enormous one we can observe and study some geographical regularities too. Thus, we may clearly see the practical illustration of the Dokuchaev—Berg's law of the geographical zonation. On the other hand it is possible for us to define precisely the system of biogeographical regions and their subdivisions for the littoral zone.

Gurjanova E., Zachs, J., Ushakov P., 1925 had shown that the limits of biogeographical regions and provinces of the Littoral of arctic seas do not coincide with the limits of biogeopgraphical subdivisions of the sumberged sublittoral zone of the Northern Polar Basin. Such a fact was known before only for sublittoral and abyssal zones: Schmardd, 1853; Ortmann, 1896; Sv. Ekman, 1935 (regarding the whole World ocean) had given the system of zoogeographical shelf for continental shelf and for abyssal bottom separately.

Gurjanova, 1951, had shown the same fact for the Northern Polar Basin.

Kussakin, 1956, has given a biogeographical subdivision of the littoral zone of the Kurilo-Sacchalin area; we may see that the limits of his littoral provinces do not coincide also with our subdivisions (Gurjanova E., 1955) of the sublittoral of this area quite exactly. Moreover, it seems to me that coincidence of limits of zoogeographical regions, provinces etc. within different vertical zones of seas can not be, that the phenomenon is quite natural and that it is a general law. By the study of some biogeographical regularities it is necessary to regard each of marine vertical zones of ocean separately and the littoral zone, of course, too.

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